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CADDISFLIES OF HISPANIOLA, WITH SPECIAL REFERENCE TO THE DOMINICAN REPUBLIC
(INSECTA: TRICHOPTERA)OLIVER S. FLINT, JR.¹JAN L. SYKORA²

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ABSTRACT

The caddisfly fauna of the Greater Antillean island of Hispaniola, comprised of the nations of the Dominican Republic and Haiti, is reviewed in light of large, new collections. As a result 109 named species are reported from the island, of which 86 or 80% are endemic to it. For comparison, Cuba has 90 named species, Jamaica 52, and Puerto Rico 42. Thirty-two species or subspecies are described and figured as new: *Austrotinodes labiatus*, *Cariboptila mathisi*, *C. paradoxa*, *Helicopsyche paraliageni*, *H. melanochaeta*, *H. poliochaeta*, *H. septifera*, *Atopsyche himulus*, *A. orientalis*, *A. peravia*, *A. thomasi*, *Streptopsyche rawlini*, *S. praecipua*, *Smicridea brunnescens*, *S. duarte*, *Alisotrichia bisetosa*, *A. woodruffi*, *A. ultima*, *Metrichia longispina*, *Ochrotrichia baorucoensis*, *O. larimar*, *O. obovata*, *O. seiba*, *Oxyethira geminata*, *O. scopulina*, *Oecetis haitises*, *Setodes anomalus*, *Marilia valga*, *Chimarra spinulifera baoruco*, *Cernotina danieli*, *Polycentropus pedernales*, and the description of *Neotrichia bifurcata* by Harris is also included. *Oxyethira simulatrix cubana* is reduced to synonymy with its nomotypical form and *Marilia nigrescens* is raised to full specific status. A number of unassociated females, 4 of which assuredly represent undescribed species, are mentioned. Synonymies, distributions and new collection data are provided for most species.

KEY WORDS: Trichoptera, new species, synonymy, distribution, Dominican Republic, Haiti, Hispaniola

INTRODUCTION

Two republics are situated on the Greater Antillean island of Hispaniola, the Dominican Republic on the eastern end and the Republic of Haiti on the western. The land area of the Dominican Republic is 48,442 sq km with a population of over 8 million, while the Republic of Haiti is about half as large with 27,750 sq km but with a population equally as large. The entire island is south of the Tropic of Cancer thus making it technically Tropical, but its climate is moderated by the surrounding seas.

Hispaniola at 76,192 sq km is the second largest Greater Antillean island after Cuba at 114,525 sq km, but much larger than Jamaica at 11,580 sq km or Puerto Rico at 8,865 sq km. In terms of elevation, the highest peak in the Greater Antilles is Pico Duarte in the Dominican Republic at 3,174 m. Blue Mountain Peak is highest on Jamaica at 2,252 m, Pico Turquino at 1,999 m is the highest point on Cuba, and Cerro de Punta at 1,338 m is the highest point on Puerto Rico. There are three primary mountain ranges in the Dominican Republic: the Cordillera Central, with Pico Duarte, is the largest and highest and continues as a series of massifs across

northern Haiti forming its northern arm; the Cordillera Septentrional follows the north coast of the Dominican Republic north of the Valle del Cibao; and the Sierra de Baoruco is found in the southwestern margin of the Dominican Republic and continues westward in Haiti as the several massifs of its southern arm. To the north of the Sierra de Baoruco is the depression of Enriquillo with its lake surface at about 40 m below sea level. This depression is bordered to the north by a lesser range, the Sierra de Neiba, which extends across central Haiti.

Geologically the island is very complex, being formed of several terranes accreted since the Late Cretaceous through the Cenozoic (Donnelly, 1988, Lewis and Draper, 1990). Some of these, such as the Sierra de Baoruco and Sierra de Neiba, are mostly limestone with few surface streams but with numerous large springs at their lower levels. The Cordilleras Central and Septentrional are of much more mixed origin with metamorphic and even extrusive rock, which is conducive to many more streams and rivers, especially at higher elevations.

TRICHOPTEROLOGICAL INVESTIGATIONS

The first caddisflies from the island were described by Walker in 1860. In addition to *Chimarra* (*Curgia*) *braconoides*, a species still recognized, he described

Phrygaena divulsa and recorded *Limnephilus griseus*. The latter two species were apparently mislabelled: *P. divulsa* is a synonym of the North American *P. cinerea*

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and *L. griseus* is European. Hagen described *Helicopsyche* (as *Notidobia*) *lutea* in 1861, a species still recognized although no new examples of this are known with certainty. August Busck of the NMNH collected insects in the Dominican Republic in 1904, including a few very rare caddisflies. His locality "S.[an] Francisco Mts." has been a puzzle to most workers but was worked out by Rehn and Hebard (1927). No further species were described until the work of Banks. In a series of three papers (1924, 1938, 1941) he described nine species from the island, the majority of which were collected by P.J. Darlington during his coleopterological work on the island (the type of *Limnephilus toussianti* Banks 1924 was reportedly from Haiti, but the species recently has been found by Ruiter 1995 to be a synonym of the Mexican *L. solidus*). Flint made a collecting trip to the island in 1969, the results of which were augmented by trips of his coworkers, the Davises in 1973 and the Spanglers in 1984. Subsequent field work by Flint and Mathis in 1995 and 1999 has added even more material, but these collections have not been worked in a coherent manner, although individual species and genera have been described. In 1979 Botosaneanu made a trip to

Haiti and in 1995 he collected the Dominican Republic extensively. The results of these expeditions were manifest in three papers: Botosaneanu 1991a, 1995, and 1996. Between 1987 and 1995 Rawlins and his coworkers at the Carnegie Museum made 6 collecting trips to the island resulting in many thousands of specimens. Woodruff of the Florida Department of Agriculture and the Florida State Collection of Arthropods made many trips to the island in the last 20 years, primarily to collect scarab beetles, but the light traps he operated also collected many caddisflies. In addition to the species described from the island, another 16 species described from other Antillean islands or the mainland have been recorded from Hispaniola up to now. The Dominican amber also contains a variety of caddisfly species, 22 species having been described in the last 15 years.

The island's caddisfly fauna was summarized in 1999 by Flint and Pérez-Gelabert. They listed 77 extant species, plus the 22 in Dominican amber, placed in 26 genera in 11 families. More recently Botosaneanu (2002) published an annotated checklist of the caddisflies of all the Caribbean islands, including Trinidad and Tobago.

FAUNISTICS

This study enumerates 109 named species of recent caddisflies for the island, and an additional 22 species are known from Dominican amber. A number of still-unassociated females or larvae are found in the collections; some may be the opposite sex of species known only from males, but four are certainly still-undescribed species in the genera *Macrouema*, *Smicridea*, *Oxyethira* and *Xiphocentron*. It would seem reasonable to expect another 20 to 50 species exist on the island, especially considering the largely uncollected northern highlands of Haiti.

Of these 109 species, 87 or 80% have been taken only on Hispaniola. Another 12 species, 11% more, are limited to Hispaniola and one or more of the other Greater Antillean islands, thus 91% of the insular fauna is endemic to the Greater Antilles. Another four species, or 4%, also range only into the Lesser Antilles, and the final six species, 6%, also include a continental component in their range. Within the Greater Antillean islands, 15 species also are found on Cuba (three only on these two islands), 12 also on Jamaica (none on these two islands only), and 13 on Puerto Rico (five on these two islands only). The greater number of species restricted to Hispaniola and Puerto Rico compared to Hispaniola and Cuba may be a result of the still very poorly known fauna of Cuba, especially from Oriente.

The Hispaniolian fauna, now 109 species, may be compared to that of Cuba, 90 species (Flint, 1996b), Jamaica, 52 species (Botosaneanu and Hyslop, 1998), and Puerto Rico, 42 species (Flint, 1992). More undescribed

species are known from all of the Greater Antillean islands, but it is reasonable to expect that the proportions will remain about the same, with the two largest islands containing twice as many species as Jamaica, which will have 10–20 species more than Puerto Rico. The major Lesser Antillean islands will probably support about as many species as Puerto Rico. The two best known islands, Guadeloupe and Dominica, each are known to contain almost 40 species, with the other, more poorly known islands, only recording numbers from 13 to 22 (Flint and Sykora, 1993). The fauna of Trinidad and Tobago is quite different from that of the Lesser Antilles, being more closely related to the continental fauna, as would be expected from their geological history (Flint, 1996a).

All except one of the species ranging outside the Greater Antilles are Hydroptilidae, the microcaddisflies. These are very small insects, most only a few millimeters in length. It is proposed that they are easily carried by the winds between the islands and the mainland. The last widely distributed form, which may be a complex of cryptic species, *Oecetis inconspicua* (Walker), is of wide ecological tolerance, being known from lentic and lotic waters over North, Central, and South America. It is suggested that the ecological tolerance of this species permits it to find suitable breeding sites whenever it is wafted to new regions. The majority of caddisflies are a bit too large to be carried easily by winds and/or have more restricted ecological tolerances that make colonization of new regions very difficult.

MATERIAL STUDIED

Although the majority of the material studied comes from three institutions, all material available to us has been included in this survey. Material from this study may be found in the following institutions.

AMNH—American Museum of Natural History, New York, NY, USA

CMNH—Carnegie Museum of Natural History, Pittsburgh, PA, USA

FCSA—Florida State Collection of Arthropods, Gainesville, FL, USA

MCZ—Museum of Comparative Zoology, Cambridge, MA, USA

NMNH—National Museum of Natural History, Washington, DC, USA

ZMUA—Zoölogisch Museum, Universiteit van Amsterdam, Amsterdam, The Netherlands

SYSTEMATIC ENTOMOLOGY

Family Calamoceratidae
Genus *Phylloicus* Müller

This genus is limited to the New World where it is widely distributed. It enters the United States only in the southwestern tier of states, but is then generally distributed far into southern Chile, and over both the Greater and Lesser Antilles. The larvae and their distinctive, flat cases made of leaf fragments placed in dorsal and ventral rows are well known (Flint, 1968a, Wiggins, 1996). They feed by shredding plant material in more slowly flowing sections of streams.

Phylloicus iridescens Banks

Phylloicus iridescens Banks, 1941:397, fig. 12 [♂]. Flint, 1967:18, figs. 85, 86 [♂, lectotype]; Botosaneanu, 1996:20 [distribution].

Phylloicus superbus Banks: Botosaneanu, 1996:21.

This species appears to be endemic to the Dominican Republic. It is usually found at intermediate and higher elevation in the mountains. In coloration it is quite variable (although less variable at a given site). The typical form has two narrow, golden bands across the forewing, the outermost not reaching the posterior margin of the wing. In some material the bands are even narrower, and the outer band is reduced to a small, comma-shaped mark from the anterior margin, and some have even lost the outer band totally. The types and other recorded material were from the Province of La Vega; we here add Dajabón and Monseñor Nouel.

Material Examined.—DOMINICAN REPUBLIC. **Dajabón Province:** 13 km S Loma de Cabrera, 20–22 May 1973, D. & M. Davis, 3♂, 2♀ (NMNH). **La Vega Province:** 20 km S Constanza [on road to Valle Nuevo], 3–7 June 1969, Flint & Gómez, 3♂, 2♀ (NMNH). La Ciénega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 1♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 6♂ (FSCA, NMNH). Arroyo El Dulce, Jarabacoa-Manabao, Cordillera Central, 26 April 1995, L. Botosaneanu, light, 1♀ (ZMUA). **La Vega-Monseñor Nouel Provinces:** Loma el Casabito, summit, 19°03'N, 70°31'W, 1390 m, 19–23 November 1992, Rawlins et al., 1♂ (CMNH). **Monseñor Nouel Province:** 1 km E Paso Alto de Casabito, 7 km NW La Ceiba, 19°02'N, 70°29'W, 1130 m, 28 July 1992, Rawlins et al., 1♀ (CMNH). [not La Vega Province as labelled], 6 km [not mi as labelled] NW of Rt. 1 on rd. to Constanza, 27 June 1998, Woodruff & Baranowski, 3♂, 1♀ (FSCA).

Phylloicus pulchrus Flint

Phylloicus pulchrus Flint, 1964:65, fig. 18 A–L.

Phylloicus superbus Banks: Botosaneanu, 1996:21, fig. 54 [♂, misidentification of material from Dominican Republic].

This species was described from Puerto Rico and is here recorded from Hispaniola for the first time. The Hispaniolan examples have been compared side-by-side with the Puerto Rican material and found to agree in coloration (and in its variations) as well as male genitalia. The species is widespread over the island from foothills to the high sierra. It is here recorded from the Provinces of Barahona, Dajabón, Elías Piña, El Seibo, La Vega, Monte Plata, and Pedernales.

Material Examined.—DOMINICAN REPUBLIC. [**Barahona Province:** San Rafael, 8.3 km S of Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 11 May 1995, Flint, 1♂ (NMNH). Nr. Filipinas, Larimar Mine, 6–11 July 1993, Woodruff, 1♂ (FSCA). **Dajabón Province:** 13 km S Loma de Cabrera, 20–22 May 1973, D. & M. Davis, 2♂, 1♀ (NMNH). **Elías Piña Province:** 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 1♂ (NMNH). **El Seibo Province:** Loma Cocuyo, 6 km N Pedro Sánchez, 18°55'N, 69°07'W, 475 m, 4 July 1992, Rawlins et al., 1♂ (CMNH). **Independencia Province:** La Descubierta, 18°34.1'N, 71°43.8'W, 0 m, 25 March 1999, Flint, 1♀ (NMNH); same, but 6 May 1995, L. Botosaneanu, light, 1♂ (ZMUA). **La Vega Province:** Río Baiguat, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 1♂ (NMNH); same, but 19–21 May 1995, 1♂, 1♀ (NMNH). 5 km SSE Jarabacoa, 640 m, 25 July 1987, Rawlins, 1♂ (CMNH). **Monte Plata Province:** Arroyo Los Verros, Sierra de Agua, 29 April 1995, L. Botosaneanu, light, 2♀ (ZMUA). **Pedernales Province:** Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 17 July 1992, 230 m, Rawlins et al., 3♂, 1♀ (CMNH). Stream & falls, 19 km N Pedernales, 230 m, 18°09.2'N, 71°44.8'W, 19 March 1999, Flint, 3♂ (NMNH).

Family Ecnomidae
Genus *Austrotinodes* Schmid

This genus is found exclusively in the New World, where it is the only member of its family. One group of species is limited to the Chilean Subregion, while a second group is widespread outside of this subregion from Texas to Uruguay (Flint, 1973). Species are known from Cuba, Tobago and now Hispaniola in the Antilles. Larvae and pupae of species in this genus have been described a number of times (Bowles, 1995, Flint, 1973, Wiggins, 1996). The larvae probably construct silken shelters attached to rocks in the bottoms of the streams wherein they live.

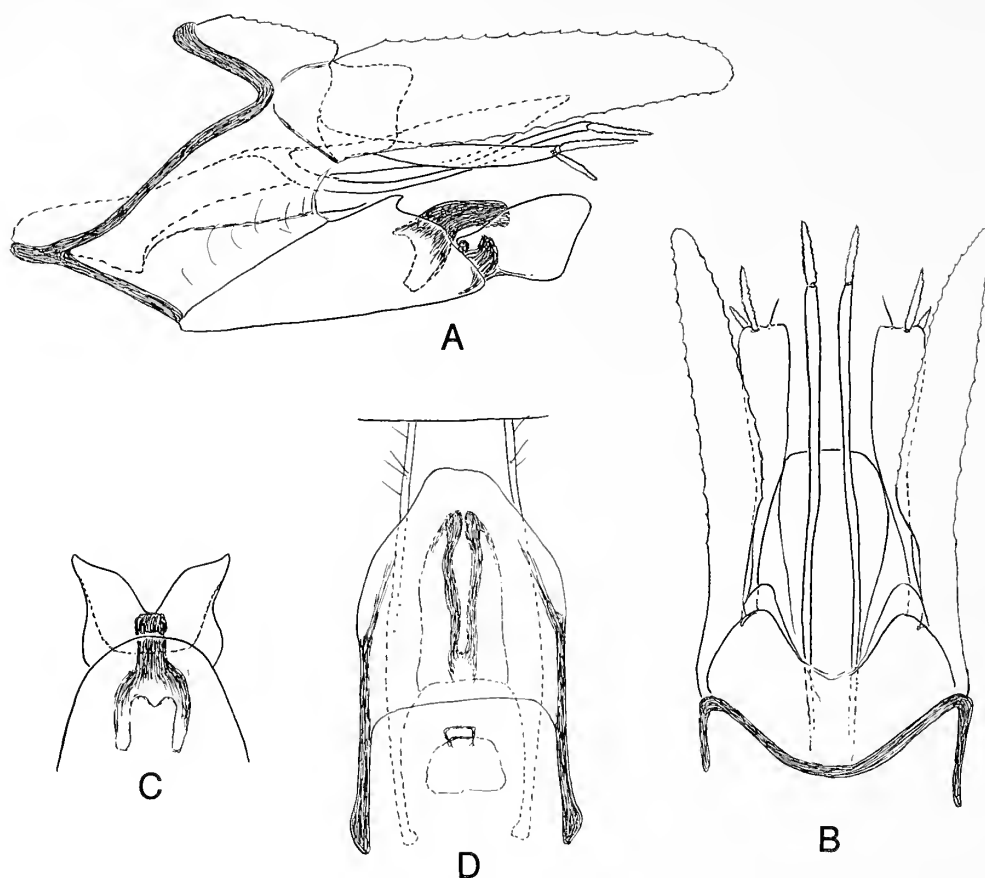


Fig. 1.—*Austrocinodes labiatus* new species, male genitalia: A, Lateral. B, Dorsal. C, Inferior appendages, ventral. Female genitalia: D, Ventral.

Austrocinodes labiatus Flint and Sykora, **new species**
(Fig. 1)

Austrocinodes species Kumanski, 1987:11 [mention of undescribed species from Dominican Republic]. Flint and Denning, 1989:109 [♀ listed].

Males of this species were discovered in one of the final lots examined, although the females were known from the beginning of the study and the description originally prepared based on this sex. The males show the species to be closely related to those from Mexico and Central America, especially *A. sedmani* Flint known from Guatemala to Costa Rica. They differ in the structure of the intermediate and inferior appendages. The females are very similar to *A. cubanus* Kumanski from Cuba, which is known from only a few females. They are related as is shown by the configuration of the eighth sternum and basal structures of the ninth segment. They may be easily distinguished by the shape of these basal structures of the ninth segment: in *A. cubanus* they are shorter and open wider apicad, while they are longer with the apices almost touching in *A. labiatus*.

Adult Male.—Length of forewing, 4 mm. Color in alcohol, brown. Genitalia: Ninth segment deeply divided laterally, sternum elongate, apical margin in ventral

aspect convex. Preanal appendage long, tapering apicad, apex rounded, surface setose, margins crenulate. Intermediate appendage slender, long, tip bearing two elongate spines; in dorsal aspect broadened apicad, apex with single spinose seta visible in addition to two elongate spines. Phallic guide heavy, black, slightly angled in middle, in ventral aspect with basal portion bifid. Inferior appendages fused basomesally, broadened apicad, posterior margin slightly oblique; in ventral aspect deeply divided mesally, flared laterad. Phallus with sclerotized base and membranous apex; dorsolaterally bearing one long, slender process on each side terminating in elongate spine.

Female.—Length of forewing, 4.5 mm. Color silvery gray; head and thorax with silvery hair, antenna cream-colored; forewing mostly grayish with darker brown spots, especially along basal half of costal margin. Genitalia: Eighth sternum strongly produced mesally, apex variable (in some examples nearly truncate others more tapered); produced into short anterolateral apodemes. Ninth sternum very long and tapering with two pairs of slender lateral sclerites bearing scattered, long setae; basally (beneath eighth sternum) with elongate, complex structure with narrow slit-like opening mesally

between pair of darkened, lip-like sclerites approximate apically. Vaginal sclerite hemispherical with small collar mesally on posterior border.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC**. **Pedernales Province**: Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al. (CMNH). Paratypes: Same data, 1♂, 6♀ (CMNH, NMNH). **Elias Piña Province**: 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 1♀ (NMNH). **Hato Mayor Province**: Parque Los Haitises, E of Trepada Alta, 12 km W El Valle, 18°59'N, 69°30'W, 145 m, 6 July 1992, Rawlins et al., 2♀ (CMNH).

Family Glossosomatidae Genus *Campsiophora* Flint

The genus is a Greater Antillean endemic and is placed in the subfamily Protoptilinae, as are all the Antillean genera. A species is known from Cuba, another from Jamaica, and the following from both Puerto Rico and Hispaniola. The larva, pupa and case was described for *C. pedophila* Flint, the type species, when it was described originally (Flint, 1964).

Campsiophora pedophila Flint

Campsiophora pedophila Flint, 1964:15, figs. 3 D–F, H–I, K–M [♂, ♀, larva, pupa, case]. Botosaneanu, 1991a:116 [Haiti]; Botosaneanu, 1995:6 [Dominican Republic].

This species was described from Puerto Rico and more recently recorded from Haiti and the Province of La Vega in the Dominican Republic. The species is here recorded also from the Provinces of Azua, El Seibo, La Altagracia, Monseñor Nouel, Monte Plata, Pedernales, Puerto Plata, and San Cristobal, which would indicate its widespread occurrence over low and intermediate elevations on the island.

Material Examined.—**DOMINICAN REPUBLIC**. **Azua Province**: Río Las Cuevas, 8 km NE Padre Las Casas, 19°46'N, 70°53'W, 580 m, 7 August 1990, Rawlins & Thompson, 2♀ (CMNH); same, but 3–4 October 1992, 9♂, 37♀ (CMNH). **Sec. Canoa**, Mirador de la Presa, Jaqui del Sur, 30 September 1978, Woodruff, 2♀ (FSCA). **Elias Piña Province**: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 3♂, 39♀ (FSCA). **El Seibo Province**: Pedro Sánchez, small stream, 10 June 1976, Woodruff, 20♂, 17♀ (FSCA, NMNH). **La Altagracia Province**: La Laguna Nisibón at Río Maimón, 18 June 1998, blacklight, Woodruff & Freytag, 100's ♂♂ ♀♀ (FSCA, NMNH); same, but sweeping, 1♂, 5♀ (FSCA). 2 km E Nisibón, Río Nisibón, 12 June 1986, Woodruff & Stange, 5♂ (FSCA). **La Vega Province**: Jarabacoa, 3–4 June 1969, Flint & Gómez, 10♀ (NMNH). Río Camú, 19 km NE of Jarabacoa, 3–4 June 1969, Flint & Gómez, 1♂, 6♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 7 May 1995, Flint, 4♀ (NMNH). Río Baiguarte, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 100's ♂♂ ♀♀ (NMNH, CMNH); same, but 19–21 May 1995, 13♂, 64♀ (NMNH). Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 6♀ (NMNH). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 2♀ (FSCA). **Monseñor Nouel Province**: Bonao, Hotel Jacaranda, 27–28 June 1998, blacklight, Woodruff & Baranowski, 100 ♂♂ ♀♀ (FSCA, NMNH). **Monte Plata Province**: Bayaguana, 22 August–2 September 1991, Brown, 7♀ (FSCA). **Pedernales Province**: Río Mulito, 21 km N Pedernales, 280 m, 18°09.3'N, 71°45.6'W, 16 May 1995, Flint, 1♀

(NMNH); same, but 18 March 1999, 10♀ (NMNH); same, but 20 March 1999, 6♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 1♀ (CMNH). **Stream & falls**, 19 km N Pedernales, 230 m, 18°09.2'N, 71°44.8'W, 19 March 1999, Flint, 29♀, plus 1♂ metamorphotype (NMNH). 20.5 km N Cabo Rojo, 12 April 2000, Woodruff & Henry, 2♂, 7♀ (FSCA). Km 21, N Cabo Rojo, 1200 ft [365 m], 1 July 1998, Woodruff & Baranowski, 2♀ (FSCA); same, but 19 June 1976, Woodruff, 4♀ (FSCA). Km 24, N Cabo Rojo, 3000 ft [915 m], 11 June 1998, Woodruff & Freytag, 8♀ (FSCA); same, but 2 July 1998, Woodruff & Baranowski, 7♀ (FSCA). **Puerto Plata Province**: Río Camú, 14 km E Puerto Plata, 17 May 1995, Flint, 2♀ (NMNH). **[San Cristóbal Province]**: at or near Naranjo Dulce, 13 km N San Cristobal, S. Francisco Mis., 27 September [1905], Aug. Busck, 2♀ (NMNH). **[Province unknown]**: Dominican Republic, intercepted Miami, 13 November 1986, Agr. # 87-265, 1♀ (NMNH).

Genus *Cariboptila* Flint

As is the case with the preceding genus, this too is limited to the Greater Antillean islands and is a member of the Protoptilinae. The type species is found on Puerto Rico, another species on Jamaica, three species are known from Cuba, and now five species from Hispaniola, all recorded only from the Dominican Republic. The larva, pupa, and case of *C. orophila* Flint from Puerto Rico have been described (Flint, 1964).

Cariboptila aurulenta Flint

Cariboptila aurulenta Flint, 1974:7, fig. 35–37 [♂]. Botosaneanu, 1996:8 [Dominican Republic].

The species was originally described from La Vega Province, and later recorded from two more localities in the same province (Botosaneanu, 1996). One more lot has now been seen, but from close to the known localities.

Material Examined.—**DOMINICAN REPUBLIC**. **La Vega Province**: La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 29♂, 70♀ (FSCA, NMNH, CMNH).

Cariboptila caab Botosaneanu

Cariboptila caab Botosaneanu, 1996:8, figs. 1–6 [♂, ♀].

This species was recently described from two localities (perhaps even identical) on the Río Mulito in Pedernales Province, and springs in La Descubierta in Independencia Province. An old collection from Elias Piña Province is here recorded, as well as new material from Barahona Province and from, and near to, the old sites.

Material Examined.—**DOMINICAN REPUBLIC**. **Barahona Province**: Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, Flint, 1♂ (NMNH). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 2♂, 1♀ (CMNH). **Elias Piña Province**: 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 13♂, 14♀ (NMNH). Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 2♂ (FSCA). **Independencia Province**: La Descubierta, 18°34.1'N, 71°43.8'W, 0 m, 25 March 1999, Flint, 1♂ (NMNH). Río Guyabal, 4.5 km N Postrer Río, 150 m, 18°34.7'N, 71°37.7'W, 25 March 1999, Flint, 7♀ (NMNH). **Pedernales Province**: Río Mulito, 21 km N Pedernales, 270 m, 18°09.3'N, 71°45.6'W, 18 March 1999, Flint, 31♂, 91♀, plus 1♀ metamorphotype (NMNH); same, but 20 March 1999, 9♂, 27♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m,

17 July 1992, Rawlins et al., 1♂, 6♀ (CMNH). Stream & falls, 19 km N Pedernales, 230 m, 18°09.2'N, 71°44.8'W, 19 March 1999, Flint & Mathis, 18♀ (NMNH).

Cariboptila calcigena Flint

Cariboptila calcigena Flint, 1974:8, fig. 41–43 [♂].

This species has been taken only in the Central Cordillera, in the Province of La Vega. Another old collection has been identified recently.

Material Examined.—DOMINICAN REPUBLIC. [La Vega Province]: Constanza, 3–4,000 ft [915–1220 m], August 1938, Darlington, 1♂, 1♀ (MCZ).

Cariboptila hispaniolica Flint

Cariboptila hispaniolica Flint, 1974:8, fig. 38–40 [♂]. Botosaneanu, 1996:8 [Dominican Republic].

This species has been taken at a number of localities, all of them in the Cordillera Central, Province of La Vega, and now Azua and Elias Piña. Association of females by genitalic characters permits the addition of more examples to the original series.

Material Examined.—DOMINICAN REPUBLIC. **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 1♀ (CMNH). **Elias Piña Province:** Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 51♂, 153♀ (FSCA). **La Vega Province:** Convento, 12 km S of Constanza, 6–13 June 1969, Flint & Gómez, ♂ holotype, 1♂ paratype, 11♀ (NMNH); same, but 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 2♀ (NMNH). Jarabacoa, 3–4 June 1969, Flint & Gómez, 1♀ (NMNH); same, but 9 Jan 1985, Munroe, 3♂, 6♀ (NMNH); same, but 13 November 1984, Spangler et al., 3♂, 12♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°00.9'N, 70°33.5'W, 980 m, 7 May 1995, Flint, 6♂, 13♀ (NMNH). Río Baiguat, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 10♂, 12♀ (NMNH); same, but 19–21 May 1995, 2♂, 4♀ (NMNH). Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 100's ♂♂ ♀♀ (NMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 13♂, 60♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 12♂, 24♀ (FSCA). La Cienega, Río Yaque del Norte, 19°51.68'N, 70°51.68'W, 3640 ft. [ca. 1110 m], 29 July 1999, S. Peralta, 8♀ (NMNH). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 100's ♂♂, ♀♀ (FSCA). Near mouth Arroyo Las Dajao, 5 km E Manabao, 19°04'N, 70°45'W, 740 m, 9 October 1991, Rawlins et al., 7♂, 4♀ (CMNH). Constanza, 27 April 1978, Woodruff & Fairchild, 2♀ (FSCA). El Arroyazo, Reserva Científica Ebano Verde, 19°1.93'N, 70°32.62'W, 18 September 1999, Perez & Bastardo, 9♀ (NMNH).

Cariboptila mathisi Flint and Sykora, new species
(Fig. 2)

This previously undiscovered species was taken at two nearby localities crossing the road (rt. 12) from Carretera Duarte as it ascends the first long grade to the west on the way to Constanza. The species is related to both *C. hispaniolica* Flint and *C. caab* Botosaneanu. From both it is distinguished by the shapes of the ninth and tenth tergal lobes and process, and the phallic complex with its digitate ventrolateral lobe and especially by the pair of long, curved, black spines arising basally in the complex.

Adult Male.—Length of forewing, 3 mm. Color fuscous; forewing fuscous with reddish tinge and two small, white spots on posterior margin at mid- and 3/4 length. Sixth sternum with broad, mesal, nail-like lobe. Genitalia: Ninth segment with anterior margin slightly produced at midheight; with pair of dorsolateral rods; with dorsomesal, knoblike lobe from posterior margin. Tenth tergite elongate and broad in lateral aspect, with numerous, mesal, setate-processes and lobes in dorsal aspect and scale-like flap from base of inner face. Phallic complex with lateral plate elongate, with setate processes; from posterodorsal margin a long, terete process, sinuate in lateral aspect; internally with pair of long, curved, black spines in ventral portion, another pair of spines above basal section with basolateral point in dorsal aspect; centrally with pouch bearing small, black spines.

Female.—Length of forewing, 2 mm. Color similar to male.

Type Material.—Holotype, male: DOMINICAN REPUBLIC. **Monseñor Nouel Province:** 8.7 km W Bonao [jct. Carretera Duarte and rt. 12], 19°01.8'N, 70°29.4'W, 890 m, 10 May 1995, W.N. Mathis (NMNH). Paratypes: Same data, 5♂ (NMNH, CMNH); same, but 6.3 km W jct., 19°01.2'N, 70°28.8'W, 670 m, 6 May 1995, 1♀ (NMNH).

Cariboptila paradoxa Flint and Sykora, new species
(Fig. 3)

A single female of an unknown species from the Province of Barahona signaled the presence of yet another undescribed species. Fortunately the collections made in 1999 obtained several series containing both males and females of this most remarkable species. It is the only species of the genus or even tribe Protoptilini in which secondary sexual modifications are described in the male.

Adult Male.—Length of forewing, 2.5–3.5 mm. Color uniformly brown, legs a bit paler. Head in frontal aspect (Fig. 3D) with large rectangular area ventrad of median ocellus shining white and smooth. Antennae attached to dorsolateral angles of white area, insertions widely separated; scape slightly compressed, bearing numerous short, broad, black setae on mesal face, flagellar segments for half length of antenna bearing similar setae on inner face. Fifth sternum with dark, arcuate ridge from anterolateral angle, across venter to other angle; sixth sternum with posteromesal point. Abdomen dorsolaterally with three pairs of finger-like, eversible, membranous lobes between segments 5 and 6, 6 and 7, and 7 and 8 (lobes disappear in clearing and are seldom seen in alcoholic material). Genitalia: Ninth segment with anterior margin convex, with lightly-sclerotized structure projecting anteriorly from dorsum; dorsum developed into a pair of depressed, concave plates projecting posteriorly. Tenth tergite with numerous, small, setate-processes and lobes. Phallic complex with lateral plate slightly flared laterad, and posteroventral plate with two black, knobs, ventral-most bearing two large, black setae; internally with pair of long, curved, black spines in ventral portion, another pair

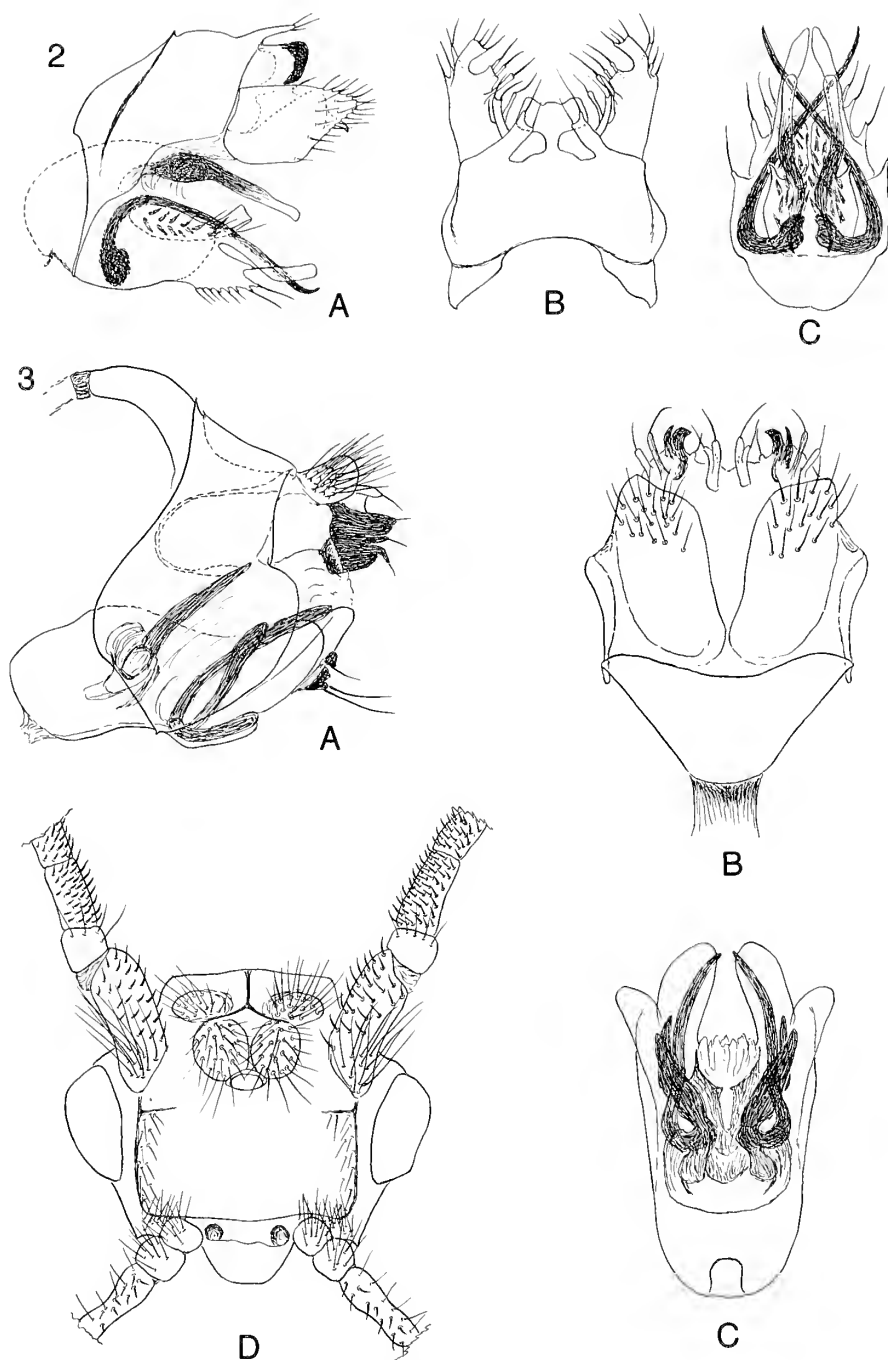


Fig. 2.—*Cariboptila mathisi* new species, male genitalia: A, Lateral. B, Dorsal. C, Phallic complex, ventral.

Fig. 3.—*Cariboptila paradoxa* new species, male genitalia: A, Lateral. B, Dorsal. C, Phallic complex, ventral. D, Head, frontal.

of spines arising near base of first pair and curving dorsolaterally around them, third pair of spines arising more basad from convoluted basal sclerite; centrally with membranous pouch extending from basolateral, sheathing sclerite.

Female.—Length of forewing, 2.5–3.5 mm. Color similar to male. Genitalia: Fifth and sixth sterna as in

male. Eighth sternum heavily sclerotized, bearing one long, straplike sclerite projecting posteriad between ninth sternites. Ninth sternum divided into a pair of strongly-sclerotized plates, each with anteromesal angle rounded and inner margin very heavily sclerotized. Vaginal sclerite ovoid, with central keyhole-like opening; with pair of internal sclerotized, ringlike structures in segments 5/6.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC**. **Independencia Province**: La Deseubierta, 18°34.1'N, 71°43.8'W, 0 m, 25 March 1999, O.S. Flint (NMNH). Paratypes: Same data, 3♂, 6♀ (NMNH, CMNH). Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, O.S. Flint, 9♂, 11♀, plus 6♂, 1♀ metamorphotypes (NMNH). **Barahona Province**: Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, O.S. Flint, 1♂ metamorphotype (NMNH). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 15♂, 6♀ (CMNH). Confluence of Río Nizaito and Río Cortico, 9.2 km NW Paraiso, 18°03'N, 71°12'W, 230 m, 9–10 August 1990, Rawlins & Thompson, 1♀ (CMNH).

Genus *Cubanoptila* Sykora

The genus is known from five extant species described from Cuba, one species from Jamaica, and three fossil species described from Dominican amber (Wichard, 1989, 1995a).

Family Helicopsychidae Genus *Helicopsyche* Siebold

The genus is very widespread over the world, found in all major faunal realms. In the New World it is found from southern Canada into southern Chile and all the larger Antillean islands. The genus was recently subject to a thorough phylogenetic study (Johanson, 1998) with the result that all the New World species are placed in two subgenera, *Cochliopsyche* which was previously considered a full genus, and *Feropsyche* a new taxon for all the New World species. Many species are found on all the islands of the Greater Antilles: Cuba, nine species; Hispaniola, ten species; Jamaica, three species; Puerto Rico, four species. They are also well represented in Dominican amber, three species having been described (Johanson and Wichard, 1996)

The larvae are well known, being the maker of the coiled, snail-shell formed case of sand grains (Flint, 1968a; Wiggins, 1996). Some Antillean species produce helical cases or snail-shell cases made almost purely of silk (Botosaneanu, 1991a, fig. 61). The larvae feed on the periphyton that they scrape off the substrate (Resh et al., 1984).

Helicopsyche (Feropsyche) altercoma Botosaneanu and Flint

Helicopsyche altercoma Botosaneanu and Flint, 1991b:178, figs. 8–16 [♂, ♀, wings]. Botosaneanu, 1991b:66, figs. 7–9 [♂, wings]; Botosaneanu, 1996:22 [distribution]; Johanson, 2002:16, fig. 5 [♂, wings].

This species has many sexual modifications in the male. The brushes of long, silky hair from the inferior appendages and dark androconia on the undersurface of the forewings have been noted before. In addition, the basal segment of the maxillary palpus has a tuft of long hairs that curve up along the face and into cephalic grooves, just as for *H. melanochaeta* n. sp. (Fig. 5E).

It is a common and widespread species on the Dominican Republic, at least in the western half of the

country, reported from the provinces of Dajabón, Elias Piña, La Vega, and San Cristobal. We here add Azua, Independencia, and Monte Cristi.

Material Examined.—**DOMINICAN REPUBLIC**. **Azua Province**: Río Las Cuevas, 8 km NE Padre Las Casas, 19°46'N, 70°53'W, 580 m, 7 August 1990, Rawlins & Thompson, 6♂, 5♀ (CMNH); same, but 3–4 October 1991, Rawlins et al., 37♂, 49♀ (CMNH). **Dajabón Province**: 9 m S Loma de Cabrera, 19°21'N, 71°37'W, 620 m, 12 July 1992, Rawlins et al., 1♂, 2♀ (CMNH). **Elias Piña Province**: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 13♂, 48♀ (FSCA). **Independencia Province**: La Descubierta, 18°34.1'N, 71°43.8'W, 0 m, 25 March 1999, Flint, 1♂ (NMNH). Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 1♂, 4♀ (NMNH). Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 2♀ (NMNH). **La Vega Province**: Convento, 12 km S of Constanza, 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 9♂, 24♀ (NMNH). Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 29♂, 146♀ (NMNH); same, but 19–21 May 1995, 3♂, 42♀ (NMNH). Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 7♂, 25♀ (NMNH). Near mouth Arroyo Los Dajaos, 5 km SE Manabao, 19°04'N, 70°45'W, 740 m, 9 October 1991, Rawlins et al., 18♂, 49♀ (CMNH). **Monte Cristi Province**: Monte Cristi, 4 June 1986, Miller & Stange, 1♀ (FSCA).

Helicopsyche (Feropsyche) dominicana Botosaneanu and Flint

Helicopsyche dominicana Botosaneanu and Flint, 1991a:200, figs. 10–16 [♂, ♀]. Botosaneanu, 1996:22 [distribution]; Johanson, 2002:118, fig. 60 [♂, wings].

This very small species does not have any apparent secondary sexual modifications of the maxillary palpi, head, wings or abdomen. It is known from La Vega and Pedernales Provinces, and we add Azua, Baoruco, Dajabón, Independencia, Monseñor Nouel, and Peravia Provinces, all on the western half of the country.

Material Examined.—**DOMINICAN REPUBLIC**. **Azua Province**: Río Las Cuevas, 8 km NE Padre Las Casas, 19°46'N, 70°53'W, 580 m, 7 August 1990, Rawlins & Thompson, 1♂ (CMNH); same, but 3–4 October 1991, Rawlins et al., 6♂, 2♀ (CMNH). **Baoruco Province**: Sierra de Neiba, Los Guineos on upper Río Colorado, 18°35'N, 71°11'W, 630 m, 11–12 August 1990, Rawlins & Thompson, 1♂, 2♀ (CMNH). **Dajabón Province**: 9 mi S Loma de Cabrera, 19°21'N, 71°37'W, 620 m, 12 July 1992, Rawlins et al., 15♂, 22♀ (CMNH). **Elias Piña Province**: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 263♂, 177♀ (FSCA). **Independencia Province**: La Descubierta, 18°34.1'N, 71°43.8'W, 0 m, 25 March 1999, Flint, 6♂, 4♀ (NMNH). **La Vega Province**: Convento, 12 km S of Constanza, 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 1♂, 2♀ (NMNH). Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 7♂, 27♀ (NMNH); same, but 19–21 May 1995, 1♀ (NMNH). Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint & Mathis, 113♂, 24♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°00.9'N, 70°33.5'W, 980 m, 7 May 1995, Flint, 1♂ (NMNH). 2.5 km SW Piñar Bonito, 18°51'N, 70°43'W, 1430 m, 26 November 1992, Rawlins et al., 47♂, 24♀, 1 w/o abdomen (CMNH). Near mouth Arroyo Las Dajaos, 5 km E Manabao, 19°04'N, 70°45'W, 740 m, 9 October 1991, Rawlins et al., 59♂, 29♀ (CMNH). **La Cienega de Manabao**, Park Headquarters, 3–5 July 1999, Woodruff, 3♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 7♂, 3♀ (FSCA). **La Cienega**, Río Yaque del Norte, 19°51.68'N, 70°51.68'W, 3640 ft [ca. 1110 m], 29 July 1999, S. Peralta, 1♂, 4♀ (NMNH). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 29♂, 31♀

(FSCA). **Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°39'N, 70°36'W, 1880 m, 5–6 August 1990, Rawlins & Thompson, 15♂, 100♀ (CMNH). [**Monseñor Nouel Province**, not La Vega Province as labelled], 6 km [not mi as labelled] NW of Rt. 1 on road to Constanza, 27 June 1998, Woodruff & Baranowski, 4♀ (FSCA).

Helicopsyche (Feropsyche) parahageni

Flint and Sykora, **new species**

(Fig. 4)

Helicopsyche hageni Banks: Botosaneanu, 1996:21 [♀, Dominican Republic, **misidentification**].

At first sight this species appears to be identical to *H. hageni* Banks from eastern Cuba. However, when cleared male genitalia of the two species are compared side-by-side, numerous differences become apparent. The most noticeable are those of the inferior appendage which is proportionately more slender and elongate basally. The mesobasal lobe is also more elongate, especially in posteroventral aspect where the mesal side is prolonged rather than almost squarely truncate as in *H. hageni*. The anterolateral angle of the ninth segment is also more nearly truncate with the lateral apodeme curved strongly ventrad with no dorsal branch. The tenth tergum is broadly rounded apically in lateral view and the apex emarginate mesally; the apicomeral arms from the tenth tergal apodeme are paired, but only single in *H. hageni*. There are no striking secondary sexual modifications in the male.

Adult Male.—Length of forewing, 3.5–4 mm. Color uniformly golden brown, paler ventrally. Maxillary palpus two segmented, bearing elongate, dark, enlarged hairs, short at apex of palpus, becoming more elongate at base of apical and entirely over basal segment. Antenna with flagellar segments encircled subapically by band of short, erect setae (producing serrate-appearing antenna). Abdominal membrane between terga and sterna with long, thin hair, especially on segments 5 & 6; third and fourth sterna barely reticulate, setal bases with large pale spots; sixth sternum lacking mesal process. Genitalia: Ninth segment narrow ventrally; anterior margin broadly produced at midheight, lobe truncate; with lateral brace strongly curved ventrad. Tenth tergum long, broadly rounded apically in lateral aspect; in dorsal aspect with apex emarginate mesally, with V-shaped, mesal apodeme, produced to apex as pair of dark marks, each side with irregular row of dark setae. Cercus ovoid. Inferior appendage narrow basally with long, gradually widening lateral section, broadened and curved posteriad dorsally, dorsal margin rounded with scattered spinose setae; apicodorsal angle pointed; in posteroventral aspect with mesal face bearing scattered spinose setae; mesobasal lobe well developed, prominent in both lateral and posterior aspects, with scattered spines. Phallus long, slender, enlarged basally, with small, C-shaped, internal, phallotremal sclerite.

Female.—Length of forewing, 4 mm. Color light brown, slightly darker than male. Abdominal membrane between terga and sterna of segments 3 & 4 covered with

long, thin hair. Abdomen otherwise as described by Botosaneanu 1996, p. 21, fig. 55.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC, [Barahona Province]**: San Rafael, 8.3 km S of Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 11 May 1995, O.S. Flint (NMNH). Paratypes: Same data, 19♂, 19♀ (NMNH). Confluence of Río Nizaito and Río Cortico, 9.2 km NW Paraiso, 18°03'N, 71°12'W, 230 m, 9–10 August 1990, Rawlins & Thompson, 163♂, 360♀ (CMNH, NMNH, FSCA). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 19♂, 151♀ (CMNH, NMNH). Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, O.S. Flint, 5♂, 22♀ (NMNH). **Independencia Province:** Río Guyabal, 4.5 km N Posrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, O.S. Flint, 6♂, 3♀ (NMNH). **Pedernales Province:** Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 117♂, 103♀ (NMNH). Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, O.S. Flint, 2♂, 2♀ (NMNH); same, but 18 March 1999, 5♂, 4♀ (NMNH); same, but 20 March 1999, 2♂, 8♀ (NMNH).

Helicopsyche (Feropsyche) haitiensis Banks

Helicopsyche haitiensis Banks, 1938:296, figs. 16, 20 [♂]. Ross, 1956:398 fig. 7 [♂]; Flint, 1967:24 [lectotype]; Johanson, 2002:69, fig. 33 [♂].

Helicopsyche haitiense Banks: Botosaneanu and Flint, 1991a:203, figs. 17–21 [♂, invalid emendation]; Botosaneanu, 1991a:134 [distribution].

No new material of this species has been seen. The type series is all male, and examination of the pinned specimens reveals no apparent secondary sexual modification of the maxillary palpi, head, wings or abdomen.

Helicopsyche (Feropsyche) kalaom Botosaneanu

Helicopsyche kalaom Botosaneanu, 1996:22, figs. 58–61 [♂]. Johanson, 2002:103, fig. 52 [♂, wings].

This recently described species was known only from La Vega Province, we now add the provinces of Peravia and Pedernales. The males have a distinct tuft of long hair arising from a pocket in the male basal maxillary palpal segment. However, there is no apparent modification of the head.

Material Examined.—**DOMINICAN REPUBLIC, La Vega Province:** La Ciénega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 1♂, 6♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 1♂, 2♀ (NMNH). Bayacanes, 120 m, 24 July 1987, Rawlins & Davidson, 2♀ (CMNH). **Peravia Province:** 3 km SW La Nuez, tributary to Río Las Cuevas, 18°40'N, 70°36'W, 1870 m, 5–6 August 1990, Rawlins & Thompson, 1♂, 3♀ (CMNH). 3 km SW La Nuez, upper Río Las Cuevas, 18°39'N, 70°36'W, 1880 m, 5–6 August 1990, Rawlins & Thompson, 10♂, 4♀ (CMNH, NMNH). **Pedernales Province:** 31 km NNE Cabo Rojo, 18°07'N, 71°35'W, 1345m, 27 September 1991, Rawlins et al., 3♂, 2♀ (CMNH, NMNH).

Helicopsyche (Feropsyche) lutea (Hagen)

Notidobia lutea Hagen, 1861:271.

Helicopsyche lutea (Hagen): Hagen, 1866:254; Ross, 1952:35 [lectotype]; Flint, 1967:24 [discussion]; Botosaneanu and Flint, 1991b:181, figs. 17–20 [♀]; Johanson, 2002:138, fig. 72 [♀].

There is no good match for this species in any of the new material. The paratype was cleared to see if it differed

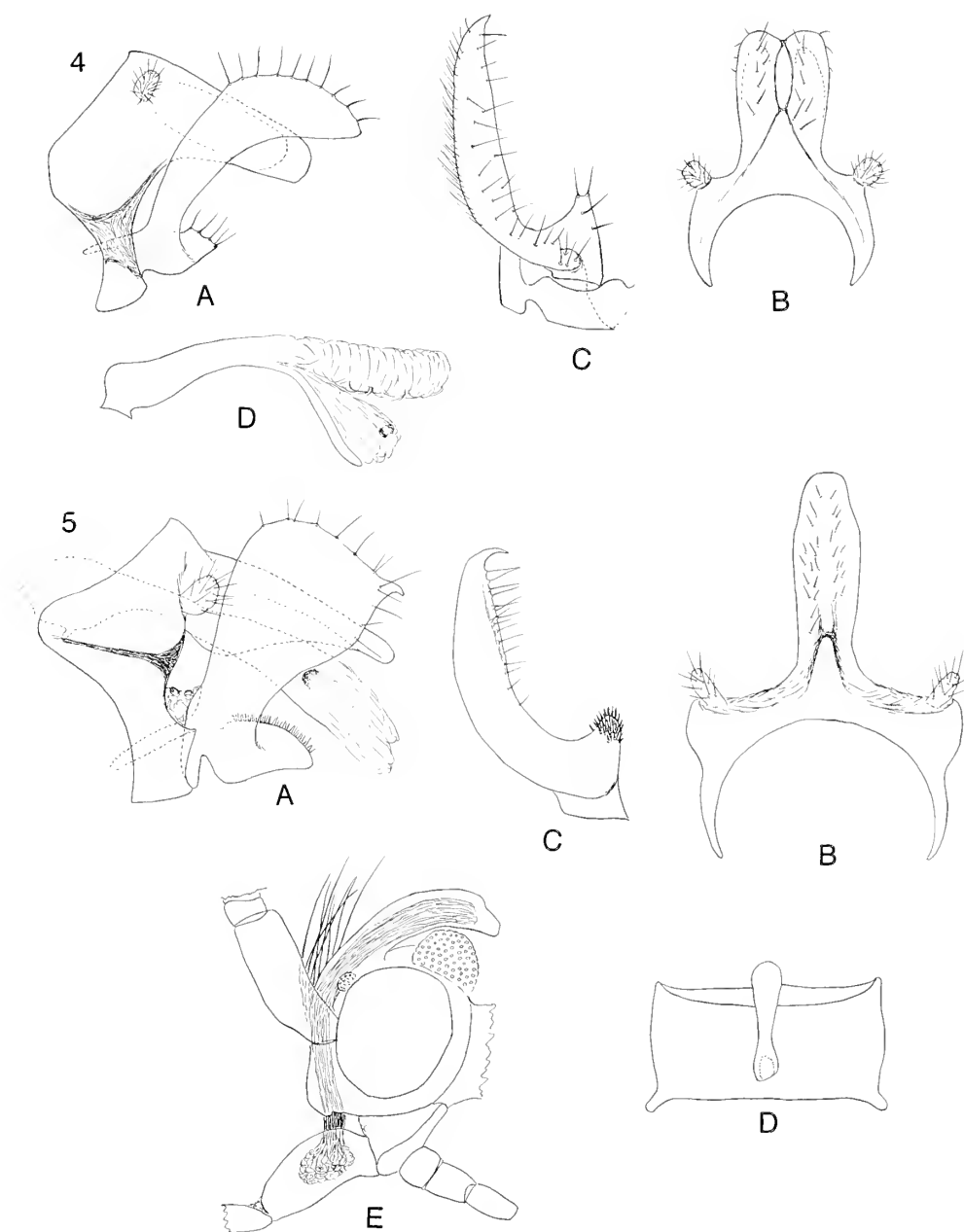


Fig. 4.—*Helicopsyche parahageni* new species, male genitalia: A, Lateral. B, Dorsal. C, Inferior appendage, posteroventral. D, Phallus, lateral.

Fig. 5.—*Helicopsyche melanochaeta* new species, male genitalia: A, Lateral. B, Dorsal. C, Inferior appendage, posteroventral. D, Sixth sternum, ventral. E, Head, lateral.

from the lectotype: it matches perfectly except that it is less damaged from handling. The following characters are apparent from this specimen: lateral abdominal membranes hairy; abdominal sterna 2–6 with strong posterior brushes, progressively denser toward 6; 6th sternal process large, terete, apex rounded; 7th sternum with anterior margin moderately W-shaped, with elongate, spinose hair across entire venter, oblique bars only slightly darkened, broad, barely noticeable; 8th sternum

almost uniformly covered with elongate, spinose setae. Otherwise all other parts of the abdomen and genitalia appear as in *H. altercoma*.

Helicopsyche (Feropsyche) nigrisensilla
Botosaneanu and Flint

Helicopsyche nigrisensilla Botosaneanu and Flint, 1991a:210, figs. 43–49 [♂, ♀]. Botosaneanu, 1996:22 [distribution]; Johanson, 2002:109, fig. 55 [♂].

The species is known only from the Dominican Republic at higher elevations in the Cordillera Central in the provinces of La Vega and now Peravia. The male does not seem to have any secondary sexual modifications of maxillary palpi, head, wings or abdomen.

Material Examined.—DOMINICAN REPUBLIC. **La Vega Province:** 2.5 km SW Piñar Bonito, 18°51'N, 70°43'W, 1430 m, 26 November 1992, Rawlins et al., 2♂, 2♀ (CMNH). Reserva Científica Valle Nuevo, Sector La Nevera. 3 km WNW La Nuez, 18°42'N, 70°36'W., 2200 m, 7 October 1991, Rawlins et al., 3♂ (CMNH). 8 km SE Constanza, near Valle Nuevo, 18°50'N, 70°42'W, 1930 m, 17 August 1990, Rawlins & Thompson, 1♂, 1♀ (CMNH). 11.5 km S. of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, Flint, 10♂, 10♀ (NMNH). **Peravia Province:** 3 km SW La Nuez, tributary to Río Las Cuevas, 18°40'N, 70°36'W, 1870 m, 5–6 August 1990, Rawlins & Thompson, 5♂, 1♀ (CMNH). 3 km SW La Nuez, upper Río Las Cuevas, 18°39'N, 70°36'W, 1880 m, 5–6 August 1990, Rawlins & Thompson, 1♂, 5♀ (CMNH).

Helicopsyche (Feropsyche) melanochaeta
Flint and Sykora, **new species**
(Fig. 5)

Helicopsyche sp. indet. ex “gr. *comosa*” Botosaneanu, 1996:22, fig. 56, 57 [♀].

This large species of *Helicopsyche* has been taken at both the far western and eastern ends of the Dominican Republic, but only at low elevations. It, *H. comosa* Kingsolver, *H. poliochaeta*, and *H. altercoma*, form a distinctive group in which the hair pencil of the basal maxillary palpal segment is enclosed in a cephalic groove. Recently Botosaneanu and Hyslop (1998) reported a similar modification in *H. ochthothephila* Flint and *H. falcigona* Botosaneanu and Flint, but in these species the basal maxillary palpal segment bears a hair pencil similar to that of *H. kalaom*, but the setae of the laterofrontal warts are elongate, black and produced posteriad into the cephalic groove which is not as tubular as in *H. melanochaeta*.

Helicopsyche poliochaeta is undoubtedly the most closely related species to *H. melanochaeta* based on the modifications of the head and maxillary palpi and the male inferior appendages. *Helicopsyche melanochaeta* is to be recognized by the intensely black coloration of the palpal hair brush, the larger mesobasal lobe of the inferior appendage and the long tenth tergum with an irregular row of setae on each side.

Adult Male.—Length of forewing, 5.5 mm. Color uniformly dark brown, paler ventrally. Maxillary palpus with basal segment widened, bearing dense tuft of very long, black, enlarged hairs from pocket on dorsomesal face near base; these hair pencils fitting into groove formed mesally in face and vertex of head by parallel carinas produced dorsad and posteriad from cephalic groove and meeting mesally, and extend posteriad just beyond rear of head. Internally a tubular opening is formed which can be opened dorsally where the two halves meet. Abdominal membrane between terga and sterna with long, thin hair; third and fourth sterna covered with very dense, strong reticulations, sterna 5–7 with dark

bordered pale spots around setal bases; sixth sternum with large mesal process as long as sternum, posterior margin densely hairy. Genitalia: Ninth segment narrow dorsally and ventrally; anterior margin strongly produced at midheight; with lateral brace not reaching anterior margin. Tenth tergum very long and slender, high basally; in dorsal aspect with tip narrowly rounded, with narrow U-shaped mark basally, each side with irregular row of short setae. Cercus ovoid. Inferior appendage broadened dorsally, dorsal margin rounded with scattered spinose setae; apicodorsal angle produced into sharp tooth, posterior margin sinuate, in posterior aspect with mesal face bearing scattered, spinose setae from protuberant bases; mesobasal lobe well developed, prominent in both lateral and posterior aspects, densely covered with short spines. Phallus very long, slender, enlarged basally, with small C-shaped internal, phallotremal sclerite.

Female.—Length of forewing, 6.5–8 mm. Color similar to male. Abdominal membrane between terga and sterna densely covered with long, thin hair; third and fourth sterna covered with very dense, strong reticulations; sterna 5 & 6 with dark-bordered, pale spots around setal bases; seventh sternum with posterior margin deeply indented by broad V-shaped sclerite; eighth sternum mesally with broad, darkened sclerite having lateral margins tapered anteriorly, setal bases laterad of this sclerite surrounded by dark-bordered, pale spots. Sixth sternum with mesal process half as long as sternum. Genitalia: Ninth segment anterolaterally with elongate, darkened, alveolar patch; ventrally with pair of large, rounded sclerites. Vaginal sclerites of usual form.

Type Material.—Holotype, male: DOMINICAN REPUBLIC. **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, O.S. Flint (NMNH). Paratypes: Same data, 9♀ (NMNH); same, but 18 March 1999, 8♀ (NMNH); same, but 20 March 1999, 53♀ (NMNH). Río Mulito, 2 km from Mencia de Pedernales, Sierra de Baoruco, 5 May 1995, L. Botosaneanu, light, ♀ (ZMUA). **Barahona Province:** confluence of Río Nizaito and Río Cortico, 9.2 km NW Paraiso, 18°03'N, 71°12'W, 230 m, 9–10 August 1990, Rawlins & Thompson, 2♂, 2♀ (CMNH). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 36♂, 12♀ (CMNH, NMNH). **La Altagracia Province:** Río Nisibón, 2 km E Nisibón, 12 June 1986, Woodruff & Stange, 1♂, 2♀ (FSCA).

Helicopsyche (Feropsyche) poliochaeta
Flint and Sykora, **new species**
(Fig. 6)

Another member of the *H. comosa* group, this species is closely allied to *H. melanochaeta*. It differs from the latter species in that the hair pencil from the maxillary palpus is pale in color, the mesobasal lobe of the inferior appendage is small with few spines, and the tenth tergum is short with a single row of setae on each side.

Adult Male.—Length of forewing, 4 mm. Color uniformly brown, paler ventrally. Maxillary palpus with basal segment widened, bearing dense tuft of very long, pale gray, enlarged hairs from pocket on dorsomesal face near base; second pair of similar hair pencils arising on

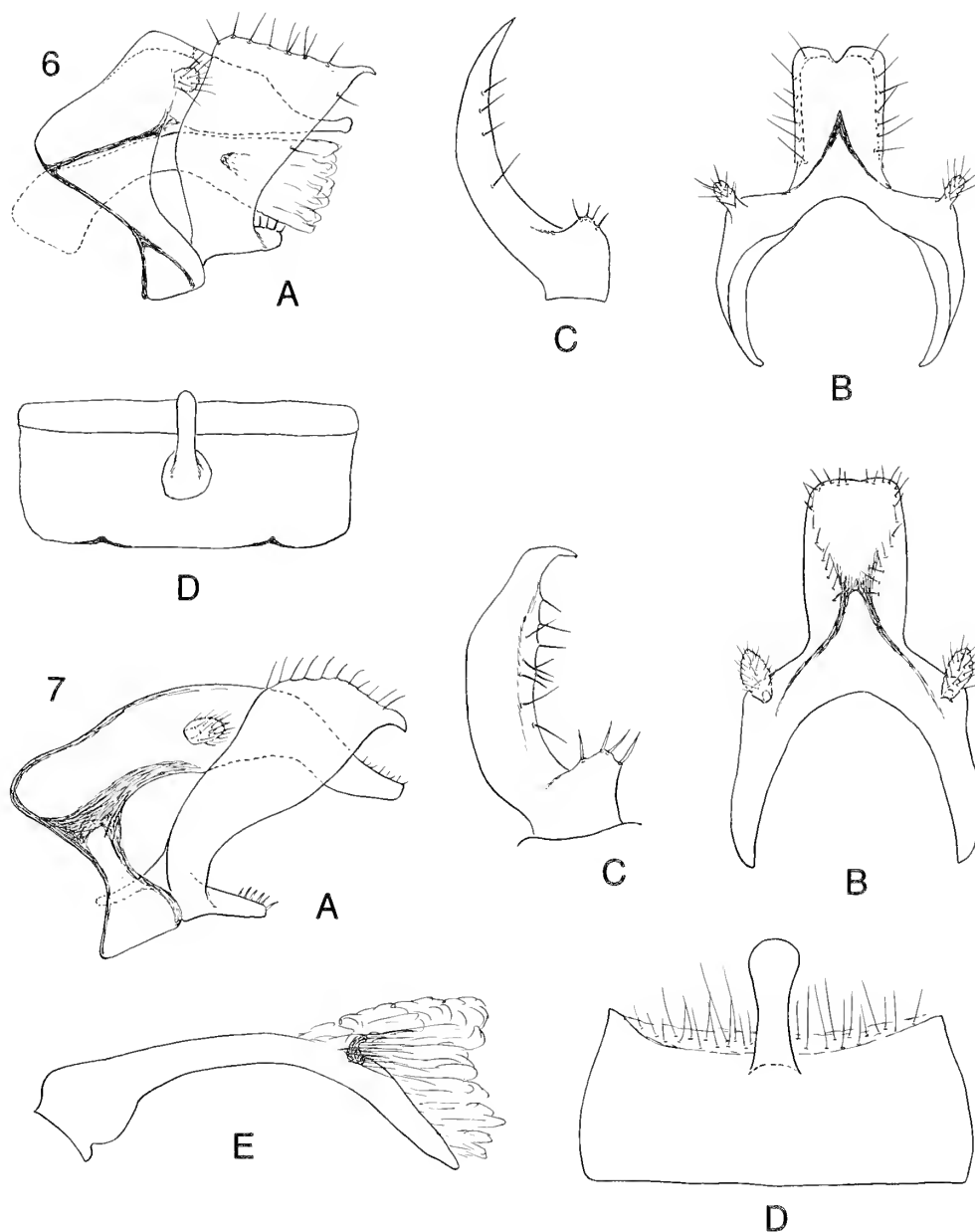


Fig. 6.—*Helicopsyche poliochaeta* new species, male genitalia: A, Lateral. B, Dorsal. C, Inferior appendage, posteroventral. D, Sixth sternum, ventral.

Fig. 7.—*Helicopsyche septifera* new species, male genitalia: A, Lateral. B, Dorsal. C, Inferior appendage, posteroventral. D, Sixth sternum, ventral. E, Phallus, lateral.

front beneath antennae, these two pairs of hair pencils fitting into groove formed mesally in face and vertex of head by parallel carinas produced dorsad and posteriad, meeting mesally, and extending posteriad almost to rear of head. Internally a tubular opening is formed which can be opened dorsally where the two halves meet. Abdominal membrane between terga and sterna with sparse, long, thin hair; third and fourth sterna covered with dense reticulations; fifth sternum with few, indistinct reticulations, sterna 5–7 with dark spots around setal bases; sixth sternum with

large mesal process as long as sternum arising from enlarged base, posterior margin sparsely hairy. Genitalia: Ninth segment narrowed dorsally and ventrally, dorsolaterally with low carina, seen in lateral aspect; anterior margin strongly produced at midheight; with lateral brace oblique, joining anterior brace along anterior margin, anterior brace extending obliquely ventrad across sternal region to posterior margin. Tenth tergum long and slender in dorsal aspect with tip shallowly bifid, with V-shaped mark basally, each side with row of spinose setae along

margin. Cercus, small ovoid. Inferior appendage broadened dorsally, dorsal margin nearly straight with scattered spinose setae; apicodorsal angle produced into sharp tooth, posterior margin straight; in posterior aspect with mesal face bearing few spinose setae; mesobasal lobe small, seen in both lateral and posterior aspects, with few short, thick spines. Phallus long, slender, enlarged basally, with small C-shaped internal, phallotremal sclerite.

Female.—Length of forewing, 4.5–5 mm. Color similar to male. Abdominal membrane between terga and sterna with long, thin hair; third sternum with single row of large reticulations; fourth sternum with 1.5 rows of large, irregular reticulations; sterna 5 and 6 with scattered setae anteriad and posterior margins with brushes of long setae; sixth sternum with short, pointed mesal process arising from much enlarged base; seventh sternum with posterior margin deeply indented by broad, indistinct, V-shaped sclerite; eighth sternum mesolaterally with scattered, long setae, posteromesally with slightly darkened, broadly V-shaped sclerite with scattered, long setae. Genitalia: Ninth segment laterally with elongate, ovoid, alveolar patch, slightly darkened. Vaginal sclerites of usual form.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC, Pedernales Province**: Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, O.S. Flint (NMNH). Paratypes: Same data, 1♂, 1♀ (NMNH); same, but 18 March 1999, 6♀ (NMNH). **Elias Piña Province**: 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 3♀ (NMNH). **El Seibo Province**: Pedro Sanchez, small stream, 10 June 1976, R.E. Woodruff, 1♀ (FSCA). **La Altagracia Province**: Río Nisibón, 2 km E Nisibón, 12 June 1986, R. Woodruff & L. Stange, 4♂, 6♀ (FSCA, NMNH).

Helicopsyche (Feropsyche) septifera
Flint and Sykora, new species
(Fig. 7)

Helicopsyche cf. *minima* Von Siebold: Botosaneanu, 1996:22 [?].

This species is very closely related to *H. haitiensis*, and very probably is its sister species, having almost identical shapes of the inferior appendages and the ninth segment. It is to be recognized most readily by the dorsal aspect of the tenth tergum. In *H. haitiensis* the basal dark mark has a distinct, inverted Y-shape, in *H. septifera* it lacks the long, mesal posterior extension and has an anteromesal, narrow, U-shaped incision; in addition the dorsal area of *H. haitiensis* over most of its surface is covered with short setae, which in *H. septifera* are confined to a row along the side and apex, leaving the central area bare. In addition the ninth segment in *H. haitiensis* bears a distinct, oblique, ventrolateral brace which is reduced to a small spur in *H. septifera*, and the new species is smaller with forewing length of barely 4 mm rather than 7 mm.

Adult Male.—Length of forewing, 4 mm. Color pale brown, forewing paler along posterior margin. Maxillary palpus, head, and wings unmodified. Third and fourth abdominal sterna covered with distinct, large reticulations; fifth sternum with few, indistinct reticulations; sixth sternum with large mesal process as long as sternum

arising from near posterior margin of segment. Genitalia: Ninth segment narrowed ventrally, very narrow laterally, dorsally curving smoothly into tenth tergum; anterior margin strongly produced at midheight; with lateral brace oblique, joining anterior brace along anterior margin below anterolateral lobe and extending ventrad, with small spur above venter; posterior margin with strong support. Tenth tergum parallel-sided in dorsal aspect with tip truncate; its basal dark mark with anterior arms strongly divergent anteriad, narrow U-shaped pale area apically; each side with row of short, spinose setae running from U-shaped mark to lateral margin and around apex, smooth centrally. Cercus, small ovoid. Inferior appendage broadened dorsally, dorsal margin slightly convex, with scattered spinose setae; apicodorsal angle produced into sharp tooth, posterior margin straight; in posterior aspect with mesal face bearing few spinose setae; mesobasal lobe elongate, narrow in lateral aspect, about as broad as long in posteroventral aspect, with few short, thick spines dorsally. Phallus long, slender, enlarged basally, with small C-shaped internal, phallotremal sclerite.

Female.—Length of forewing, 4.5–5 mm. Color similar to male. Abdominal membrane between terga and sterna with long, thin hair; third and fourth sterna with several irregular rows of large reticulations; fifth sternum with few reticulations; sterna 5 and 6 with scattered setae anteriad and posterior margins with brushes of long setae; sixth sternum with elongate, tapering mesal process; seventh sternum with scattered setae, V-shaped sclerite barely visible; eighth sternum with numerous, long setae, posterior margin slightly darkened. Genitalia: Ninth segment laterally almost covered by dark, alveolar patch, tenth segment basolaterally with small alveolar patch. Vaginal sclerites of usual form.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC, Pedernales Province**: Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, O.S. Flint (NMNH). Paratypes: Same data, 2♀ (NMNH); same, but 18 March 1999, 1♂, 2♀ (NMNH); same, but 20 March 1999, 2♀ (NMNH). Río Mulito, 2 km from Mencia de Pedernales, Sierra de Baoruco, 5 May 1995, L. Botosaneanu, light, 2♀ (ZMUA). **Barahona Province**: confluence of Río Nizaito and Río Cortico, 9.2 km NW Paraiso, 18°03'N, 71°12'W, 230 m, 9–10 August 1990, Rawlins & Thompson, 4♀ (CMNH). Río Nizaito, 5 km NW Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, Flint, 1♀ (NMNH).

Family Hydrobiosidae
Genus *Atopsyche* Banks

Only a single genus of this family, that is lacking on the Lesser Antilles, is known from the Greater Antilles. All the Greater Antillean islands harbor at least one species: Cuba with two, Hispaniola now with nine, Jamaica with two, and Puerto Rico with one. Of the Hispaniolan species, three are known only from Haiti, and the other six only from the Dominican Republic. It seems rather surprising that from the 185 specimens of the genus collected by the Carnegie expeditions, 180 were a single new species which had not been taken in previous trips to the island.

Careful study of the female genitalia of the species reported from the Dominican Republic has allowed firm association of the sexes for all the species known from the central and eastern areas of the island and thus produced a few more confirmed records for those species. As a result, an additional species from the Cordillera Oriental near the eastern corner of the country has come to light. The presence of the genus in Dominican amber has been recorded by Wichard (1987), but no species are yet described.

The larvae are well known, having been described a number of times: Botosaneanu and Sykora, 1973; Flint, 1963; Wiggins, 1996. They are typical inhabitants of cool, lotic waters and are primarily predators on other arthropods.

Atopsyche batesi Banks

Atopsyche batesi Banks 1938:304, fig. 29 [♂]. Ross and King, 1952:198, fig. 16 [♂].

Collections from the type locality have produced a second collection of this species, 50 years after the types were taken. All lots are from La Visite in the Massif de la Selle, in the southeastern extremity of Haiti close to the Dominican border.

Material Examined.—HAITI. [Département de L'Ouest]: La Visite & vic., La Selle Range, 5–7000 ft. [1525–2135 m], 16–23 Sept. 1934, M. Bates, ♂ holotype, ♂ paratype (MCZ). Parc National La Visite, Pic La Visite, 2100 m, 11 May 1984, blacklight, Thomas, 4♂, 2♀ (FSCA, NMNH); same, but basecamp, 1980 m, 19 May 1984, 1♀ (FSCA).

Atopsyche conventica Flint

Atopsyche conventica Flint 1974:4, figs. 18–20 [♂].

The association of the females of this species enlarges the series from the type locality and produces a few new records, most from the same general region in the Province of La Vega but also one from the Province of Elias Piña.

Material Examined.—DOMINICAN REPUBLIC. **Elias Piña Province**: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 5♀ (FSCA, NMNH). **La Vega Province**: Convento, 12 km S of Constanza, 6–13 June 1969, Flint & Gómez, ♂ holotype, 1♂ paratype, 7♀ (NMNH). La Palma, 12 km E El Río, 2–13 June 1969, Flint & Gómez, 5♀ (NMNH). Constanza, Hotel Nueva Suiza, 29 May 1973, D. & M. Davis, 1♀ (NMNH). Constanza to Jarabacoa, 2–4,000 ft. [610–1220 m], August 1938, Darlington, 2♀ (MCZ). La Ciénega de Manabao, Park Headquarters, 20–21 April 2000, Woodruff & Henry, 25♀ (FSCA, NMNH). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 1♂, 2♀ (FSCA).

Atopsyche davisorum Flint

Atopsyche davisorum Flint 1974:4, figs 21–23 [♂].

The known range of this species is extended from that of the holotype, Elias Piña, to include the Provinces of Dajabón and Peravia.

Material Examined.—DOMINICAN REPUBLIC. **Dajabón Province**: 13 km S Loma de Cabrera, 20–22 May 1973, D. & M. Davis, 2♀ (NMNH). 9 km S Loma de Cabrera, 12 July 1992, Rawlins et al., 1♀

(CMNH). **Peravia Province**: 3 km SW La Nuez, upper Río Las Cuevas, 5–6 August 1990, Rawlins & Thompson, 2♀ (CMNH); same, but 5–6 Oct 1991, Rawlins et al., 1♀ (CMNH).

Atopsyche hinnulus Flint and Sykora, new species (Fig. 8)

This, the smallest species of the genus yet discovered on Hispaniola, was taken near the Haitian border inland from the Caribbean coast.

Atopsyche hinnulus is another member of the *A. batesi* Group, but is otherwise very distinctive. It does have a much shortened filicercus and marks an intermediate condition between those species with long filicerci, such as *A. conventica*, and *A. batesi* which lacks the filicercus. It is the only known Hispaniolan species with a short filicercus, but the Jamaican *A. brachycerca* Flint, which is otherwise not closely related, likewise has a short filicercus. The very long apical segment of the inferior appendage with a short dorsal lobe and basomesal, pointed flap from the basal segment are unique features among the insular species.

Adult Male.—Length of forewing, 5–5.5 mm. Color brown, with oblique pale, transverse band near mid-length bordered apically by narrow dark band, apical half slightly paler than basal half, with some pale mottling. No veins with scale-like setae. Third tergum with anterior third modified, impressed and covered with short, specialized setae; fourth tergum unmodified. Fifth sternum with short anterolateral process barely half as long as its segment. Sixth sternum with posteromesal process reaching posterior margin of seventh sternum; seventh sternal process slightly longer than one-fourth of its sternum. Genitalia: Ninth segment with anterolateral margin produced and angulate; posteroventrally produced beneath inferior appendage. Tenth tergum membranous, typical of genus. Paracercus narrowing apicad, dorsal margin produced into erect, apical and subapical teeth. Filicercus short, tubular, half length of paracercus; cercus buttonlike with a short stalk. Inferior appendage with basal segment bearing basomesal shelf-like flap ending in apicomesal point and projecting slightly ventrad of segment in lateral aspect, apicodorsally produced into short, broad lobe dorsally covering base of apical segment; apical segment long, tapering apicad, especially in ventral aspect, bearing shallow mesal carina from base. Phallus with base elongate, broad, bearing articulated dorsal process; phallosomal beaks developed as elongate, ventral, spines curved sharply dorsad, in dorsal aspect each with subapical point born from ventral margin; mesally with single, straight spine.

Female.—Length of forewing, 6–7 mm. Color as in male.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. Pedernales Province**: Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 270 m, 18 March 1999, O.S. Flint (NMNH). Paratypes: Same data, 1♂, 8♀ (NMNH, CMNH); same, but 20 March 1999, 5♀

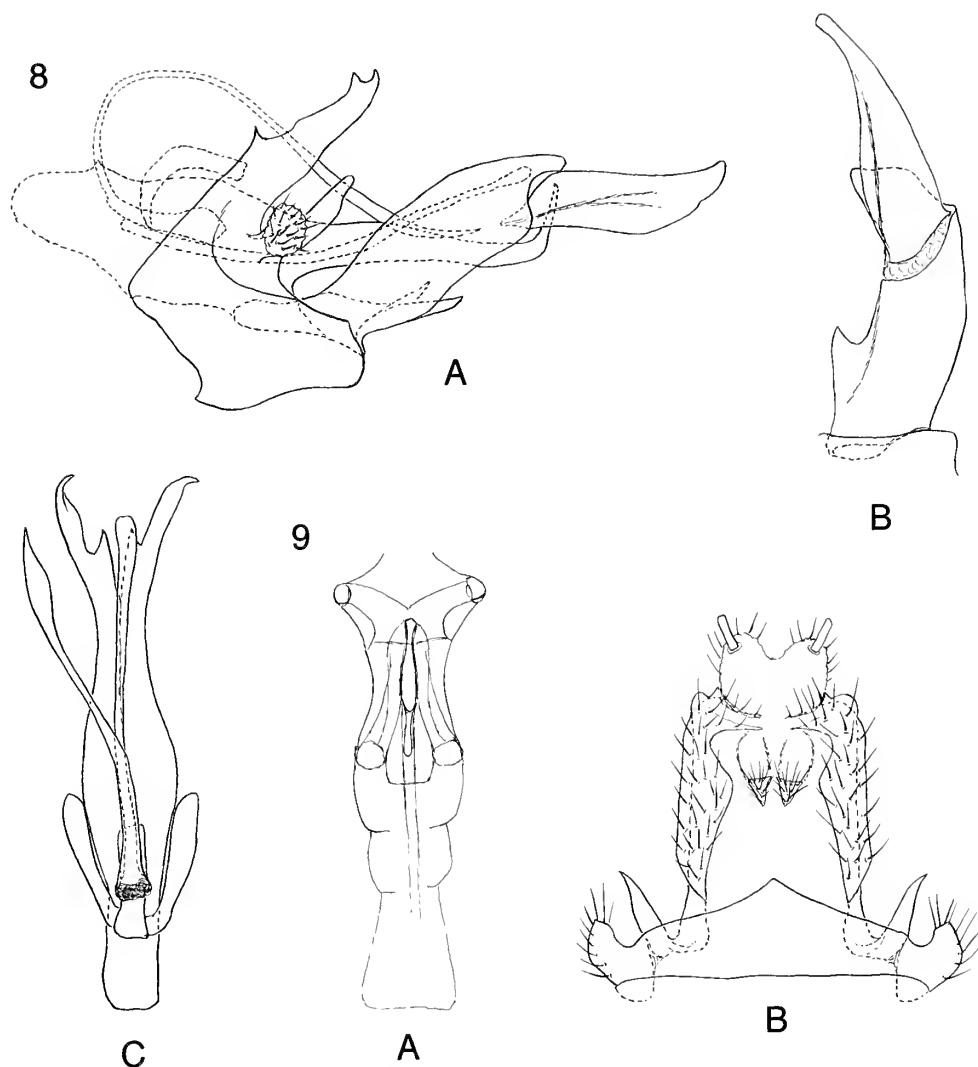


Fig. 8.—*Atopsyche hinulius* new species, male genitalia: A, Lateral. B, Inferior appendage, posteroventral. C, Phallus, dorsal.

Fig. 9.—*Atopsyche orientalis* new species, female genitalia: A, Vaginal sclerites, ventral. B, 8th, 9th, and 10th segments, ventral.

(NMNH). Along Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, riparian woodland, J. Rawlins, S. Thompson, C. Young, R. Davidson, 8♂ (CMNH, NMNH).

Atopsyche lilicae Botosaneanu

Atopsyche lilicae Botosaneanu 1991a: 114, figs. 3–6 [♂]

This species is still known only from the types collected in central Haiti.

Material Examined.—HAITI. Département de L'Ouest: "Le Saut d'Eau" (Ville Bonheur), 27 November 1979, L. Botosaneanu, 1♂ paratype (ZMUA).

Atopsyche orientalis Flint and Sykora, new species (Fig. 9)

We depart from our usual procedure to describe this species from a female only. All the other species known

from the Dominican Republic have their females known and readily distinguishable. *Atopsyche orientalis* is totally distinct from them all in its genital structure.

The coloration of *A. orientalis* is very pale with a dark basal triangle resting on the costal margin, only similar to the female of *A. davisorum*, but it is paler yet. The females of *A. taina* Flint also taken at the same site, are very dark winged. The genitalia of *A. orientalis* differ from those of the other insular species in lacking a setate sclerite mesally on the fused ninth-tenth sternal area and in the possession of the basolateral, leaf-like, frec sclerite from the tenth segment, as well as the details of the vaginal sclerites.

Adult Male.—Unknown.

Female.—Length of forewing, 6.5 mm. Color: Head and thorax with cream-colored hair and sclerites; forewing mostly cream-colored, with basal, brown triangle

broadest on costal margin, some darker marking apicad, especially on costal margin. Third and fifth abdominal segments unmodified; sixth segment with small, anterolateral, projecting angle, apicomeral process reaching posterior margin of seventh segment; apicomeral process of seventh segment very short, barely one-fourth length of segment; eighth sternum obtusely angulate and densely hairy mesally. Genitalia: Ninth segment with distinct posterolateral lobe, posterior margin broadly angulate mesally, lacking any mesal sclerite bearing setae. Tenth segment invaginated basolaterally, with a free-standing, leaf-like sclerite produced posteriad; sclerotized and setate laterally with pair of small setate sclerites posteromesally. Vaginal sclerites complex: with elongate, slit-like mesal opening giving rise to pair of slender apodemes anteriad; laterally almost parallel-sided, convoluted, posterolaterally with small arm-like sclerites.

Type Material.—Holotype, female: **DOMINICAN REPUBLIC. El Seibo Province:** 15 km S Miches, ca. 500 m, 31 May 1973, D. & M. Davis (NMNH).

Atopsyche peravia Flint and Sykora, **new species**
(Fig. 10)

This previously unknown species was taken in large numbers by several of the Carnegie Museum expeditions in the provinces of Peravia, La Vega, and on the border between La Vega and Monseñor Nouel.

Atopsyche peravia is very closely related to the Haitian *A. batesi*, but is distinguished by the elongate, slender apices of the clasper segments, by the shape of the apex of the phallus which is turned sharply laterad in dorsal aspect, and by the broader and more serrate apex of the paracercus. The very long and slender filicercus of *A. peravia* is lacking on the type of *A. batesi*. The lectotype of *A. batesi* was examined with care to see if these structure were broken off in the type. No broken basal remanent is present nor is there any clear tear in the sclerites at this point; there does seem to be a very small nipple, hardly as long as wide, at this point, supporting the assumption that the filicercus is truly lacking in *A. batesi*.

Adult Male.—Length of forewing, 7–10.5 mm. Color dark brown, almost fuscous; forewing dark brown, with some narrow, oblique pale bands and mottling, pale subapically. No veins with scale-like setae. Third tergum with anterior third modified, impressed and covered with short, specialized setae; fourth tergum with similar modification, but only for anterior fourth. Fifth sternum with long anterolateral process reaching to middle of seventh sternum. Sixth sternum with posteromesal process reaching posterior margin of seventh sternum; seventh sternal process slightly longer than half of its sternum. Genitalia: Ninth segment with anterolateral margin produced into small lobe; posteroventrally strongly produced. Tenth tergum membranous, typical of genus. Paracercus broad, dorsal margin produced into

small dorsal and subapical teeth. Filicercus long and slender, surpassing paracercus; cercus buttonlike with short stalk. Inferior appendage with basal segment slightly inflated at midlength, apex produced into a long, slender, dorsomesal process; apical segment long and slender, surpassing dorsomesal process. Phallus with base elongate, narrow, bearing articulated dorsal process; phallosheath beaks developed as ventral, hook-like spine curved dorsad and subapical shoulder produced laterad and spinulose; mesally with single, straight spine.

Female.—Length of forewing, 9–11.5 mm. Color more strongly marked with pale areas than male; forewing with pale, basal semicircular mark and oblique pale band from near base to midlength on anterior margin, setting off dark, triangular area centered on anterior margin, apical two-thirds heavily mottled with pale markings.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°39'N, 70°36'W, 1880 m, cloud forest on river, 5–6 October 1991, J. Rawlins, R. Davidson, C. Young, & S. Thompson (CMNH). Paratypes: Same data, 2♂, 40♀ (CMNH, NMNH); same, but 2 September 1995, Rawlins et al., 1♂ (CMNH); same, 5–6 August 1990, 32♂, 94♀ (CMNH, NMNH, FSCA). **La Vega Province:** 2.5 km SW Piñar Bonito, 18°51'N, 70°43'W, 1430 m, riparian vegetation near stream in pine woodland, 26 November 1992, Rawlins et al., 1♂, 1♀ (CMNH). 9 km SE Constanza, near Valle Nuevo, 18°50'N, 70°42'W, 1930 m, 17 August 1990, Rawlins & Thompson, 3♂, 1♀ (CMNH, NMNH). 18 km SE Constanza, 18°46'N, 70°39'W, 2310 m, pine woodland near head of small stream, 25 November 1992, Rawlins et al., 1♂ (CMNH). 23 km SE Constanza, 18°45'N, 70°37'W, 2225 m, grassland with pines and scattered marshes, 24–25 November 1992, Rawlins et al., 1♂ (CMNH). Reserva Científica Valle Nuevo, Sector La Nevera, 3 km WNW La Nuez, 18°42'N, 70°36'W, 2200 m, mesic pine woodland, 7 October 1991, Rawlins et al., 6♂, 1♀ (CMNH, NMNH). **La Vega-Monseñor Nouel Provinces:** Loma el Casabito, summit, 19°03'N, 70°31'W, 1390 m, cloud forest, 19–23 November 1992, Rawlins et al., 6♂, 4♀ (CMNH, NMNH).

Atopsyche taina Flint

Atopsyche taina Flint 1974:4, figs. 15–17 [♂].

The original male types of this species were from the Provinces of La Vega and Dajabón. The new records extend the range into El Seibo and probably Santiago Provinces and add a female to the Dajabón locality.

Material Examined.—**DOMINICAN REPUBLIC. Dajabón Province:** 13 km S Loma de Cabrera, 20–22 May 1973, D. & M. Davis, 1♂ paratype, 1♀ (NMNH). **El Seibo Province:** 15 km S Miches, 31 May 1973, D. & M. Davis, 2♀ (NMNH). **La Vega Province:** La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 1♂ (FSCA). [**Santiago Province**, probably]: foothills Cordillera Central, S of Santiago, June 1938, Darlington, 1♀ (MCZ).

Atopsyche thomasi Flint and Sykora, **new species**
(Fig. 11)

Atopsyche thomasi is very closely related to the Haitian *A. lilicae*, but is distinguished by several differences in the male genitalia. The apex of the paracercus is more elongate and bears a distinct lateral spine subapically in

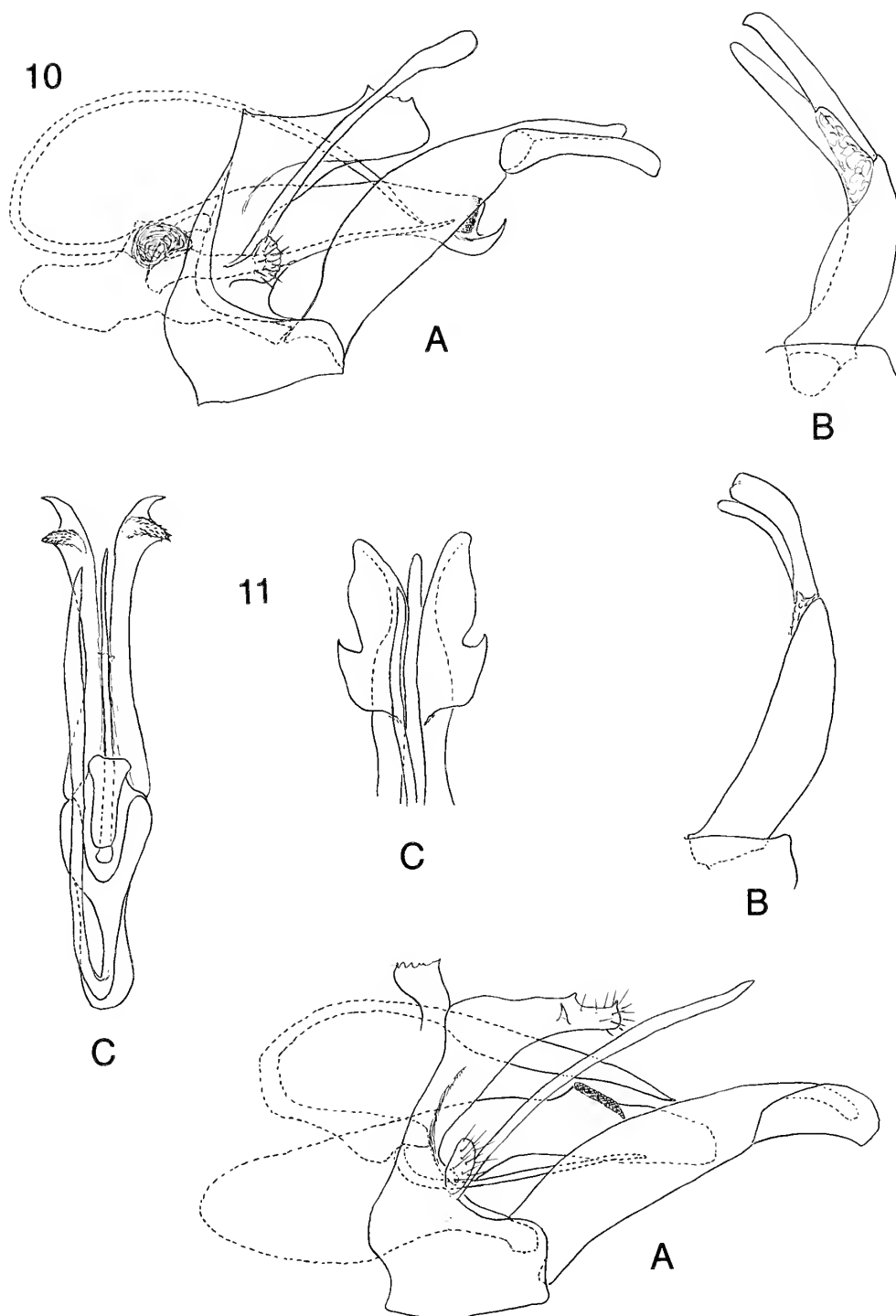


Fig. 10.—*Atopsyche peravia* new species, male genitalia: A, Lateral. B, Inferior appendage, posteroventral. C, Phallus, dorsal.

Fig. 11.—*Atopsyche thomasi* new species, male genitalia: A, Lateral. B, Inferior appendage, posteroventral. C, Tip of phallus, dorsal.

A. thomasi. The major difference is seen in the dorsal, subapical lobes of the phallus which in *A. lilicae* extend straight out from the phallus in the form of a tapering, apically pointed, flap, but in *A. thomasi* they are broad and

shallow with the apex hooked posteriad. Also the apex of the inferior appendage is only slightly enlarged and rounded in *A. thomasi*, but more clearly broadened and bearing a small nipple-like lobe in *A. lilicae*.

The types of *A. lilicae* are from the north of the Enriquillo Depression and that of *A. thomasi* from the south. It seems possible that this is another vicariant pair separated by this depression such as *Streptopsyche parander* (Botosaneanu) and *S. davisorum* Ross and Unzicker.

Adult Male.—Length of forewing, 7.5 mm. Color in alcohol dark brown; forewing dark brown, with some pale mottling, especially along veins. No veins with scale-like setae. Third tergum with anterior third modified, bearing four impressed areas filled with short, specialized setae (as shown by Botosaneanu, 1991a, fig. 3). Fifth sternum with long anterolateral process reaching to anterior margin of seventh sternum. Sixth sternum with posteromesal process reaching posterior margin of seventh sternum; seventh sternal process slightly longer than half of its sternum. Genitalia: Ninth segment with anterolateral margin sinuate; posteroventrally strongly produced. Tenth tergum membranous, typical of genus. Paracercus cylindrical, elongate, with small anteapical teeth, one on dorsal margin other lateroventrally. Filicercus long and slender, surpassing paracercus; cercus ovoid. Inferior appendage with basal segment almost three times as long as wide; apex produced into long, slender, dorsomesal process; apical segment elongate, slightly enlarged subapically, tip rounded. Phallus with base elongate, bearing articulated dorsal process; phallosome beaks developed subapically as dorsal flaps, in dorsal aspect shallow and elongate each with tip produced into sharp point directed posteriad; mesally with single, straight spine.

Female.—Unknown.

Type Material.—Holotype, male: **HAITI, Département de l'Ouest:** saddle between Fe Noir and Enfer, 1700 m. 16 May 1984, M.C. Thomas (FSCA).

Atopsyche species

We have seen single females of two species of the genus from the extreme southwestern parts of Haiti and the Dominican Republic. Their genitalia are different from those of any of the species whose females are known, but *A. lilicae* and *A. thomasi* are known only from males and occur in the southern half of Haiti. For this reason these females are left undescribed.

Material Examined.—**HAITI, Département du Sud:** Ville Formon, 31 km NW Les Cayes, s slope Morn Formon, Massif de la Hotte, 18°20'N, 74°01'W, 1405 m, 2–8 September 1995, Rawlins et al., 1♀ (CMNH).

DOMINICAN REPUBLIC, Barahona Province: Nr. Filipinas, Larimar Mine, 3300 ft [ca. 1205m], 12 April 1997, Woodruff, 1♀ (FSCA).

Family Hydropsychidae Genus *Calosopsyche* Ross and Unzicker

This is a genus of limited distribution. Species are found on the islands of Cuba and Hispaniola and in

Central America from Costa Rica and Panama. Four species are described from Cuba, and four from Hispaniola, two of which are limited to the Dominican Republic and two to Haiti. Both of the Haitian species are known from only the unique female holotypes. The amber fossil, *Palaehydropsyche fossilis*, would appear to be somewhere in the lineage of this (Wichard, 1986). The immature stages of the continental *C. continentalis* are described (Flint and Bueno, 1987), as are those of the Cuban *C. cubana* (Botosaneanu, 1994b).

Calosopsyche batesi (Flint)

Hydropsyche batesi Flint, 1962:25, fig. 6 [♀].

Calosopsyche batesi (Flint): Ross and Unzicker, 1977:309; Flint and Bueno, 1987:33 [listed].

This species is still known only from the unique female holotype taken in the La Selle Range in southeastern Haiti.

Calosopsyche bohio (Botosaneanu)

Hydropsyche bohio Botosaneanu, 1991a:132, fig. 58, 59 [♀].

Calosopsyche bohio (Botosaneanu). Flint et al., 1999:75 [to *Calosopsyche*].

This species is still known only from the unique female holotype taken at the Saut d'Eau in the Département de l'Ouest in central Haiti. However, it is possible that the male of this species is described herein as *Streptopsyche praecipua* n. sp.

Calosopsyche carinifera (Flint)

Hydropsyche carinifera Flint, 1962:27, fig. 7 [♀]. Botosaneanu, 1996:17.

Calosopsyche carinifera (Flint). Ross and Unzicker, 1977:309; Flint and Bueno, 1987:34, figs. 5, 6 [♀].

Originally described from the locality "foothills of the Cordillera Central, south of Santiago," its more recent records are all from elevations of over 1000 meters in the Cordillera Central. It is thus difficult to assess the location/elevation of the original record. It is now known from the Provinces of La Vega, Monseñor Nouel, Peravia, and San Juan, with the original record probably referable to the Province of Santiago.

Material Examined.—**DOMINICAN REPUBLIC, La Vega Province:** Reserva Científica Valle Nuevo, Sector La Nevera, 3 km WNW La Nuez, 18°42'N, 70°36'W, 2200 m, 7 October 1992, Rawlins et al., 1♀ (CMNH). **La Vega-Monseñor Nouel Provinces:** Loma El Casabito, summit, 19°03'N, 70°31'W, 1390 m, 19–23 Nov 1992, Rawlins et al., 3♂, 3♀ (CMNH). **Monseñor Nouel Province** [not La Vega Province as labelled]: 6 km [not mi. as labelled] NW of Rt. 1 on rd. to Constanza, 27 June 1998, Woodruff & Baranowski, 30♂, 39♀ (FSCA, NMNH). Paso Alto de Casabito, 8 km NW La Ceiba, 19°02', 70°29'W, 1280 m, 28 July 1992, Rawlins et al., 1♂, 1♀ (CMNH). 1 km E Paso Alto de Casabito, 7 km NW La Ceiba, 19°02'N, 70°29'W, 1130 m, 28 July 1992, Rawlins et al., 12♂, 10♀ (CMNH, NMNH). **Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°39'N, 70°36'W, 1880 m, cloud forest on river, 5–6 August 1990, Rawlins & Thompson, 10♂, 182♀ (CMNH, NMNH); same, but 2 September 1995, Rawlins et al., 2♂, 4♀ (CMNH); same, but 5–6 October 1991, 21♂, 167♀ (CMNH, NMNH); same but tributary to Río Las

Cuevas, 1870 m, 18°40'N, 70°36'W, 5–6 August 1990, 2♀ (CMNH). **San Juan Province:** 7 km N Arroyo Caño, 1 km S Los Frios, 18°52', 71°01'W, 1120 m, 1 September 1995, Rawlins et al., 1♂ (CMNH).

Calosopsyche domingensis (Banks)

Hydropsyche domingensis Banks, 1941:398, figs. 32–34 [♂]. Flint, 1962:24, fig. 4 [♀]; Flint, 1967:12 [lectotype]; Botosaneanu, 1996:17, figs. 37–41 [♂, ♀].

Plectropsyche domingensis (Banks): Ross and Unzicker, 1977:308.

Calosopsyche domingensis (Banks): Flint, et al., 1999:75 [nomenclature].

This is a widespread species in the Dominican Republic, generally found in larger rivers and streams usually below 1000 meters, but sometimes occurring up to 1500 m in the Cordillera Central. It is now known from the Provinces of Azua, Dajabón, Elias Piña, La Vega, Monseñor Nouel, Monte Cristi, Puerto Plata, and Santiago.

The species is provisionally placed in the genus *Calosopsyche*, with which its genitalia are in best agreement. However, many aspects of the genitalia are very distinctive and with full knowledge of all the Antillean species, their immature stages, and a worldwide analysis, it may be necessary to erect a new genus for this species.

Material Examined.—**DOMINICAN REPUBLIC.** **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 100's ♂♂, ♀♀ (CMNH); same, but 7 August 1990, 100's ♂♂ ♀♀ (CMNH). **Dajabón Province:** Río Massacre, Balneario Don Miguel, 7 km SW Dajabón, 40 m, 26 May 1973, D. & M. Davis, 1♀ (NMNH). 9 m S Loma de Cabrera, 19°21'N, 71°37'W, 620 m, 12 July 1992, Rawlins et al., 50 ♂♂ ♀♀ (CMNH). 13 km SE Loma de Cabrera, ca 400 m, 20–22 May 1973, D. & M. Davis, 9♂, 18♀ (NMNH). **Elias Piña Province:** 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 4♂, 3♀ (NMNH). Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 35♂, 160♀ (FSCA). North slope Sierra de Neiba, 2 km SW Canada, 7 km WSW Hondo Valle, 18°42'N, 71°45'W, 980 m, 29 August 1995, Rawlins et al., 1♀ (CMNH). **La Vega Province:** Constanza, 2–6 June 1969, Flint & Gómez, 10♂, 9♀ (NMNH). Convento, 12 km SE Constanza, 6–13 June 1969, Flint & Gómez, 2♂, 1♀ (NMNH); same, but 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 8♂, 13♀ (NMNH). Jarabacoa, 9 Jan 1985, Munroe, 2♀ (NMNH); same, but 3–4 June 1969, Flint & Gómez, 21♂, 69♀ (NMNH); same, but 600 m, 9 August 1980, Norrbom, 1♀ (CMNH); same, but Río Jimenoa, 13 November 1984, Spangler et al., 7♂, 35♀ (NMNH). Río Baiguate, 1–2 km S Jarabacoa, 8–9 May 1995, Flint, 12♂, 17♀ (NMNH); same, but 19 May, 12♂, 30♀ (NMNH). Río Baiguate, Bamboo Hole Canyon, 5 km SE Jarabacoa, 580 m, 22 July 1987, Rawlins & Davidson, 1♀ (CMNH). 5 km SSE Jarabacoa, 640 m, 25 July 1987, Rawlins, 1♂, 4♀ (CMNH). 15 km N Jarabacoa, 240 m, 21 July 1987, Rawlins & Davidson, 6♀ (CMNH). Hotel Montana, 10 km NE Jarabacoa, ca. 520 m, 28 May 1973, D. & M. Davis, 3♂, 4♀ (NMNH). Río Camú, 19 km NE of Jarabacoa, 12 June 1969, Flint & Gómez, 30♂, 62♀ (NMNH). Río Camú, 3.5 km NW La Vega, 19°13.7'N, 70°35.2'W, 100 m, 10 May 1995, Mathis, 1♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°0.9'N, 70°33.5'W, 980 m, 7 May 1995, Flint, 4♂, 11♀ (NMNH). La Palma, 12 km E of El Río, 2–13 June 1969, Flint & Gómez, 6♂, 19♀ (NMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 100's ♂♂ ♀♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 100's ♂♂ ♀♀ (FSCA). La Cienega, Río Yaque del Norte, 19°51.68'N, 70°51.68'W, 3640 ft. [ca. 1110 m], 29 July 1999, S. Peralta, 3♂, 6♀ (NMNH). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 100's ♂♂ ♀♀ (FSCA). Near mouth Arroyo Los Dajaos, 5 km SE Manabao, 19°04'N, 70°45'W, 740 m, 9 October 1991, Rawlins et al., 100's ♂♂ ♀♀

(CMNH). 2.5 km SW Piñar Bonito, 18°51'N, 70°43'W, 1430 m, 26 November 1992, Rawlins et al., 1♀ (CMNH). Bayacanes, 120 m, 24 July 1987, Rawlins & Davidson, 3♀ (CMNH). El Arroyazo, Reserva Científica Ebano Verde, 19°1.93'N, 70°32.62'W, 18 September 1999, Perez and Bastardo, 3♂, 10♀ (NMNH). **La Vega-Monseñor Nouel Provinces:** Loma El Casabito, summit, 19°03'N, 70°31'W, 1390 m, 19–23 November 1992, Rawlins et al., 1♂ (CMNH). **Monseñor Nouel Province:** Paso Alto de Casabito, 8 km NW La Ceiba, 19°02', 70°29'W, 1280 m, 28 July 1992, Rawlins et al., 1♂, 1♀ (CMNH). 1 km E Paso Alto de Casabito, 7 km NW La Ceiba, 19°02'N, 70°29'W, 1130 m, 28 July 1992, Rawlins et al., 4♂, 8♀ (CMNH). 6 km [not mi. as labelled] NW of Rt. 1 on road to Constanza, 27 June 1998, Woodruff & Baranowski, 4♂, 5♀ (FSCA). 9.2 km W Rt. 1 on Constanza Rd., 28 June 1998, Woodruff & Baranowski, 1♂, 2♀ (FSCA). Bonao, Hotel Jacaranda, 28–30 June 1999, Woodruff & Baranowski, 1♂, 4♀ (FSCA); same, but 18 April 2000, Woodruff & Henry, 5♂, 4♀ (FSCA). Río Blanco, Hydroelectric Plant, 20 km W Bonao, 600 m, 13 May 2001, Woodruff & Nuñez, 15♀ (FSCA). **Monte Cristi Province:** 10 km S Monte Cristi, 5 m, 23 May 1973, D. & M. Davis, 1♂, 5♀ (NMNH). 3 km N Villa Elisa, 1 October 1985, Woodruff & Stange, 1♂, 1♀ (FSCA). **Puerto Plata Province:** Los Hidalgos, 4–5 June 1969, Flint & Gómez, 11♂, 49♀ (NMNH). **San Cristóbal Province:** Hato Dumas, 21 October 1986, Woodruff & Frank, 1♂ (FSCA). [at or near Naranjo Dulce, 13 km N San Cristóbal]: S. Francisco Mts., September 1905, Aug. Busck, 6♀ (NMNH). **San Juan Province:** Río Mijo, 20 May 1985, Woodruff & Stange, 2♀ (FSCA). 7 km N Arroyo Caño, 1 km S Los Frios, 18°52'N, 71°01'W, 1120 m, 1 September 1995, Rawlins et al., 1♂, 6♀ (CMNH). **Santiago Province:** 1 km NE San José de Las Matas, 19°21'N, 70°56'W, 540 m, 11 July 1992, Rawlins et al., 5♂, 4♀ (CMNH). La Cumbre, 3000 ft [915 m], 25–26 April 1978, Woodruff et al., 1♀ (FSCA). Valle de Bao, 5885 ft. [ca. 1795 m], 9 July 1992, Ivie, 1♀ (NMNH).

Genus *Leptonema* Guerin

The genus contains over 100 species, the vast majority limited to the Neotropical Realm, including both the Greater and Lesser Antilles. A much smaller number of species are known from the Afrotropical Realm including Madagascar. A species is described from eastern Cuba and larvae are known from Puerto Rico. Wichard (1987) recorded the presence of three adults of this genus in Dominican amber. The larvae recorded as this genus by Botosaneanu (1991a) from the southern arm of Haiti have proven on further study to be *Macronema*, q.v.

Genus *Macronema* Pictet

This genus as presently constituted is composed of 30 described species limited to the Neotropical Realm, where it is known from Mexico to northern Argentina. It is recorded from the Greater Antillean islands of Cuba, Jamaica, and Puerto Rico. This is the first report of a species from Hispaniola. Since the record is based on larvae only, the species cannot be determined at this time.

Material Examined.—**HAITI.** **Département du Sud:** Rivière du Cavaillon, Saut Mathurine, 5 November 1979, L. Botosaneanu, 5 larvae (ZMUA).

Genus *Streptopsyche* Ross and Unzicker

This genus, now containing five species, is endemic to the island of Hispaniola. Three of the species have only been found in the Dominican Republic and the other two

only in Haiti. The immature stages of *S. parander* (Botosaneanu) are described (Flint, 2002).

Streptopsyche antilles (Ross and Palmer)

Hydropsyche antilles Ross and Palmer, 1946:184, figs. 1–4 [♂, ♀]. Flint, 1962:25, fig. 5 [♀].

Streptopsyche antilles (Ross and Palmer): Ross and Unzicker, 1977:307, figs. 19B, C [♂].

This species has only rarely been taken, and from widely separated localities. It was described from a “small mountain stream tributary to one of the rivers running to Trujillo City”; we assume that this is in the Distrito Nacional. It was later recorded from the Département de l’Ouest in Haiti and now from El Seibo, Elias Piña, and San Juan Provinces in the Dominican Republic.

Material Examined.—DOMINICAN REPUBLIC. **Elias Piña Province:** north slope Sierra de Neiba, 2 km SW Canada, 7 km WSW Hondo Valle, 18°42’N, 71°45’W, 980 m, 29 August 1995, Rawlins et al., 43♂, 62♀ (CMNH, NMNH). **El Seibo Province:** Loma Cocuyo, 6 km N Pedro Sánchez, 18°55’N, 69°07’W, 475 m, 4 July 1992, Rawlins et al., 1♀ (CMNH). **San Juan Province:** at river, 1 km off rd. to Vallejuelo, El Capá, 21 May 1985, Woodruff et al., 1♂, 1♀ (FSCA). 7 km N Arroyo Caño, 1 km S Los Frios, 18°52’N, 71°01’W, 1120 m, 1 September 1995, Rawlins et al., 1♂ (CMNH).

Streptopsyche davisorum Ross and Unzicker

Streptopsyche davisorum Ross and Unzicker, 1977:308, figs. 18A–C [♂]. Flint et al., 1999:76 [nomenclature]; Flint, 2002:409 [immatures].

Hydropsyche davisorum (Ross and Unzicker): Botosaneanu, 1996:18, figs. 42–47 [♂, ♀].

This species appears to be restricted to intermediate elevations in the Cordilleras Septentrional and Central. It was described from Elias Piña Province and recorded from Duarte Province and here from Baoruco and Dajabón Provinces. The record of a single female from La Descubierta, Independencia Province is questionable (Botosaneanu, 1996). We are unable to find diagnostic characters in the clasper groove and receptacle between this species and *S. parander*. The locality of La Descubierta is below sea level and midway between the known ranges of these two species and thus not strongly supportive of either identification. Males will be required to verify its identity.

Material Examined.—DOMINICAN REPUBLIC. **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46’N, 70°53’W, 580 m, 7 August 1990, Rawlins & Thompson, 1♀ (CMNH). **Baoruco Province:** Sierra de Neiba, Los Guineos on upper Río Colorado, 18°35’N, 71°11’W, 630 m, 11–12 August 1990, Rawlins & Thompson, 38♀ (CMNH, NMNH). **Dajabón Province:** 9 km S Loma de Cabrera, 19°21’N, 71°37’W, 620 m, 12 July 1992, Rawlins et al., 1♂, 2♀ (CMNH). 13 km S Loma de Cabrera, ca. 400 m, 20–22 May 1973, D. & M. Davis, 2♀ (NMNH). **Elias Piña Province:** north slope Sierra de Neiba, 2 km SW Canada, 7 km WSW Hondo Valle, 18°42’N, 71°45’W, 980 m, 29 August 1995, Rawlins et al., 8♂, 9♀ (CMNH, NMNH). Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 18♂, 18♀ (FSCA, NMNH). **Independencia Province:** Río Guyabal, 4.5 km N Postrer Río, 150 m, 18°34.7’N, 71°37.7’W, 25 March 1999, O.S. Flint, 1♂, 10♀, plus 18 larvae, 4 pupae, 1♂, 1♀ metamorphotypes

(NMNH). **San Juan Province:** 7 km N Arroyo Caño, 1 km S Los Frios, 18°52’N, 71°01’W, 1120 m, 1 September 1995, Rawlins et al., 9♂, 3♀ (CMNH, NMNH).

Streptopsyche parander (Botosaneanu)

Hydropsyche parander Botosaneanu, 1996:19, figs. 48–53 [♂, ♀].

Streptopsyche parander (Botosaneanu): Flint et al., 1999:76 [nomenclature]; Flint, 2002:409 [larva, pupa].

This is a species restricted to the Sierra de Baoruco, and has so far only been found in the Dominican Republic, but most assuredly must occur in the Massif de la Selle in Haiti. It is known from the three Provinces which encompass this Sierra: Barahona, Independencia, and Pedernales. At first it was thought that this might be a synonym of *C. batesi* known from a female from this range in Haiti. However, study of the type of *C. batesi* shows beyond doubt that it is a different species, and belongs in *Calosopsyche* close to *C. carinifera*.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** San Rafael, 8.3 km S Baoruco, 18°01.9’N, 71°08.4’W, 30 m, 22 March 1999, Flint, 4♂, 8♀ (NMNH). Confluence of Río Nizaito and Río Cortico, 9.2 km NW Paraíso, 18°03’N, 71°12’W, 230 m, 9–10 August 1990, Rawlins & Thompson, 12♂, 55♀ (CMNH, NMNH). Río Nizaito, 6 km NW Paraíso, 18°02’N, 71°12’W, 170 m, 25–26 July 1990, Rawlins & Thompson, 59♂, 248♀ (CMNH, NMNH). Río Nizaito, 5 km N Paraíso, 18°01.5’N, 71°11.6’W, 150 m, 21 March 1999, Flint, 2♂, 11♀, 68 larvae, 7 pupae, 2♂ metamorphotypes (NMNH). **Nr. Filipinas, Larimar Mine,** 3300 ft [ca. 1000 m], 6–11 July 1993, Woodruff, 2♂ (FSCA); same, but 12 April 1997, 1♂, 1♀ (FSCA); same, but 20–26 June 1992, Woodruff & Skelley, 1♂, 1♀ (FSCA); same, but 26 June–7 July 1992, 5♂, 1♀ (FSCA, NMNH). **Independencia Province:** Río Las Damas, 2 km S Duvergé, 18°22.0’N, 71°31.4’W, 10 m, 24 March 1999, Flint, 6♂, 5♀ (NMNH). Loma de Vientos, 4 km S Los Pinos, 18°35’N, 71°46’W, 475 m, 12 October 1991, Rawlins et al., 4♀ (CMNH). **Pedernales Province:** 14.5 km N Cabo Rojo, 18°03’N, 71°39’W, 165 m, 20 July 1990, Rawlins et al., 1♀ (CMNH). 26 km N Cabo Rojo, 18°06’N, 71°38’W, 730 m, 20 July 1990, Rawlins et al., 4♂, 4♀ (CMNH, NMNH). 21 km N Cabo Rojo, Las Mercedes, 490 m, 10 July 1987, Rawlins & Davidson, 1♀ (CMNH). Río Mulito, 21 km N Pedernales, 18°09.3’N, 71°45.6’W, 280 m, 18 March 1999, Flint, 3♂, 10♀, 18 larvae, 2 pupae, 1♂ metamorphotype (NMNH); same, but 20 March 1999, 5♀ (NMNH). Stream & falls, 19 km N Pedernales, 230 m, 18°09.2’N, 71°44.8’W, 19 March 1999, Flint, 2♀ (NMNH).

Streptopsyche rawlinsi Flint and Sykora, **new species**
(Fig. 12)

This species is related to both *S. parander* and *S. davisorum*. It is most easily distinguished from both by the structure of the endophallus. In *S. parander* this lobe is continuous with the phallobase and is long, ribbon-like and with a single apical point. In *S. davisorum* the endophallus is differentiated from the phallobase, as it is in *S. rawlinsi*, and bears two ventrally directed points. However, these points are much larger, nearly equal in size and separated by a deep sinus in *S. davisorum*; in *S. rawlinsi* they are quite small and the margin between them is slightly convex. There does not seem to be any absolutely diagnostic structure in the female clasper groove-receptacle complex that will distinguish the three species.

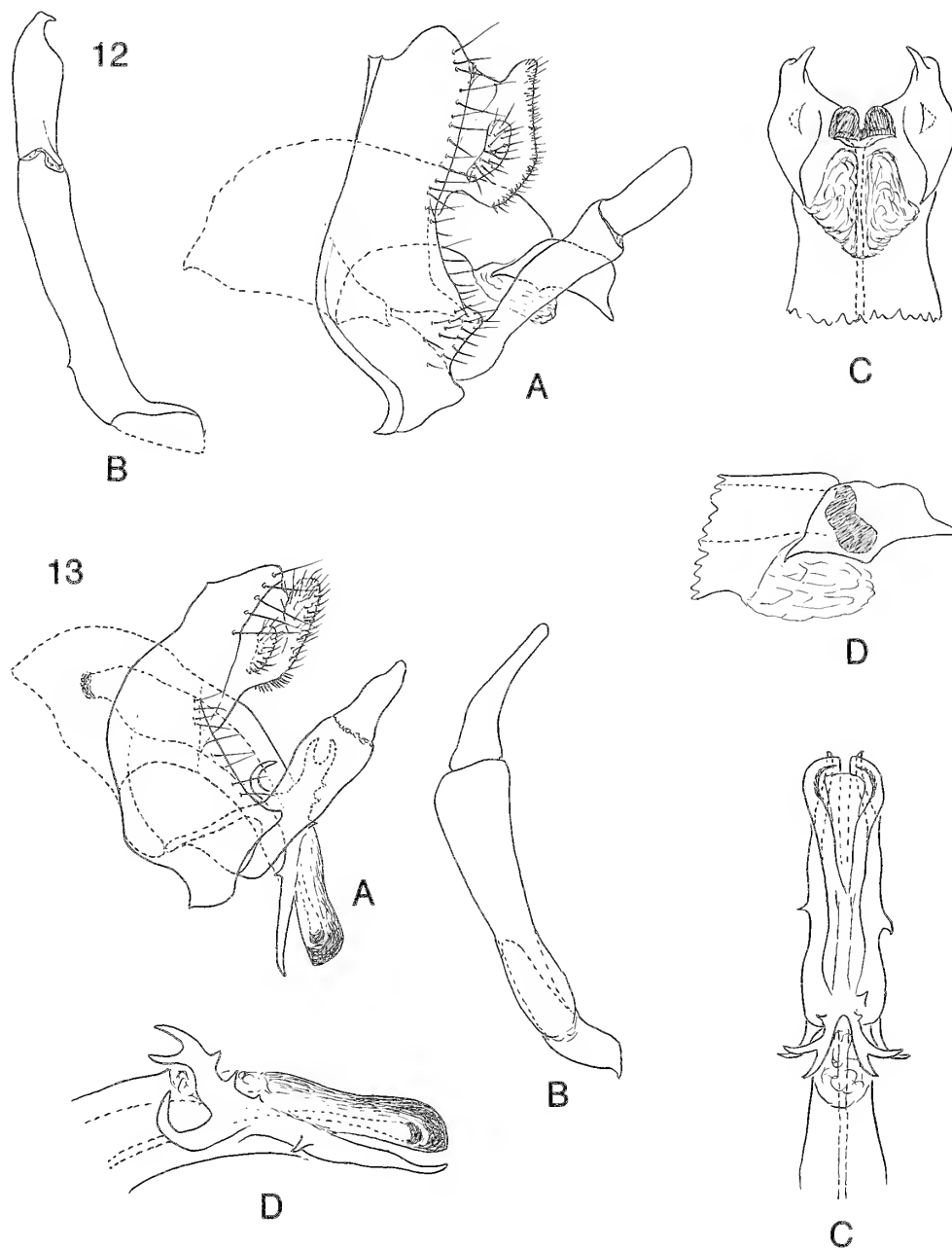


Fig. 12.—*Streptopsyche rawlini* new species, male genitalia: A, Lateral. B, Inferior appendage, posteroventral. C, Tip of phallus, ventral. D, Tip of phallus, lateral.

Fig. 13.—*Streptopsyche praecipua* new species, male genitalia: A, Lateral. B, Inferior appendage, posteroventral. C, Tip of phallus, dorsal. D, Tip of phallus, lateral.

Adult Male.—Length of forewing, 11 mm. Color grayish-brown; venter and legs pale brown; forewing grayish-brown, densely maculate with small, pale brown spots. Genitalia: Tenth tergum with warts *a* and *c* confluent along posterior margin of tergum, projecting apicodorsad, wart *b* elongate, distinct. Inferior appendage with basal segment straight, dorsal margin sinuate in lateral aspect; apical segment in ventral aspect with mesal

margin convex, apex produced into small truncate lobe with tip pointed mesad. Phallus inflated basally; endophallus produced into short, pointed lobes apicoventrally and basoventrally; phallotremal sclerites elongate, oblique, peanut-shaped.

Female.—Length of forewing, 12.5 mm. Color grayish-brown; marked as in male. Genitalia: Ninth segment very broad ventrally. Clasper groove with anterior margin

overhanging groove, filled with minute setate tubercles. Clasper receptacle deep, ovoid; ventral margin overhanging groove with dorsally directed carina and small flap posteriad of carina (not securely different from structures of *S. davisorum* and *S. parander*).

Type Material.—Holotype, male: **HAITI, Département du Sud**: S slope Morné Formon, Ville Formon, 31 km NW Les Cayes, Massif de La Hotte, 18°20'N, 74°01'W, 1405 m, 7–8 September 1995, disturbed forest and fields, J. Rawlins, R. Davidson, G. Onore (CMNH). Paratype: Same data, 1♀ (CMNH).

Streptopsyche praecipua Flint and Sykora, **new species**
(Fig. 13)

This very odd species is related most closely to *S. antilles* (Ross and Palmer), based on the endothecal process being developed into long apicoventral and basodorsal lobes. It is most easily recognized by the basodorsal lobe of the endothecal process being deeply divided and the endotheca itself being greatly produced beyond the insertion of its process.

It is quite possible that this is the male of the species described as *S. bohio* (Botosaneanu). The two types were taken only about 25 km apart, however, there is no firm evidence of this yet and until there is, it seems most advantageous to consider them distinct.

Adult Male.—Length of forewing, 9 mm. Color brown; venter and legs yellowish-brown; forewing brown, densely maculate with small, whitish spots. Genitalia: Tenth tergum with warts *a* and *c* confluent along posterior margin of tergum, projecting apicodorsad, wart *b* elongate, distinct. Inferior appendage with basal segment comparatively short, dorsal margin barely sinuate in lateral aspect; apical segment in ventral aspect tapering to elongate slender apex. Phallus inflated basally; endothecal process produced into long, slender lobe with basolateral tooth, and running posteriad beneath endotheca, basodorsal lobe bearing strong, hooklike ventral process curved dorsad and dorsal arm bifid apically, with several small teeth (opposite sides different in number and placement); endotheca produced into long tube divided apically into cuplike lobes; phallotremal sclerite small, inconspicuous.

Female.—Unknown.

Type Material.—Holotype, male: **HAITI, [Département de l'Ouest]**: Manneville, Feb 6–10 1922, about 60 ft. alt. [ca. 18 m], F. 4629. L. (AMNH).

Genus *Smicridea* McLachlan

This is a very large genus, exclusively of New World distribution. It is divided into two subgenera, the typical subgenus and the subgenus *Rhyacophylax*. They are both found on the continent from the southwestern United States south into Argentina and Chile. The typical subgenus is found on all the larger Greater and Lesser Antillean islands, but *Rhyacophylax* is not found on any of the Antillean islands. All the Greater Antillean species belong to the *S. fasciatella* Group, within which the

specific characters are limited to small differences in the genitalia and, sometimes, coloration. In addition to the five species listed here, there is a single female (MCZ) in poor condition from the Cordillera Central that appears to be yet another species. The immature stages are well known (Flint, 1964, 1968a; Wiggins, 1996).

Smicridea (Smicridea) brunnescens
Flint and Sykora, **new species**
(Fig. 14)

This is the only brown species yet discovered on Hispaniola. It thus resembles the Jamaican *S. jamaicensis* Flint, which it was thought to be for many years. Comparison of the genitalia of the two species shows that they are distinctly different. The inferior appendages in *S. jamaicensis* are distinctly angled in ventral aspect near the base, but evenly curved in *S. brunnescens*. The lateral wart on the tenth tergum in *S. brunnescens* protrudes more strongly and is rounded in lateral aspect at its base. The phallotremal sclerite is very similar in the two species but the short basal rods are divergent in *S. brunnescens*, and appressed in *S. jamaicensis*.

Adult Male.—Length of forewing, 5.5–6 mm. Color brown; venter and legs slightly paler brown; forewing brown, inconspicuously maculate with paler marking. Abdomen with four internal, reticulate sacs, each about as long as its segment. Genitalia: Ninth segment with anterior margin in lateral view vertical centrally, curving posteriad both dorsally and ventrally. Tenth tergum with tip in lateral aspect slightly produced dorsad, obliquely truncate in dorsal aspect; lateral wart rounded anteriorly in lateral aspect and protruding anteriorly in dorsal aspect. Inferior appendage with basal segment straight, slightly inflated apically in lateral aspect, evenly curved from base in ventral aspect; apical segment elongate, parallel-sided, apex obliquely truncate with small tuft of setae. Phallus tubular, curved almost directly posteriad from base; phallotremal sclerites elongate, ribbon-like in lateral aspect; with broad apicolateral “wings” in ventral aspect and with pair of small, divergent, rod-like processes anteromesally.

Female.—Length of forewing, 6–7 mm. Color brown; marked as in male. Genitalia: Ninth segment broad ventrally. Clasper groove not developed; receptacle shallow, cuplike, dorsal margin open, near posteroventral margin of segment.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC, [La Vega Province, Río Jimenoa]**: Jarabacoa, 3–4 June 1969, Flint & Gómez (NMNH). Paratypes: Same data, 12♂, 31♀ (NMNH, CMNH). Río Camú, 19 km NE Jarabacoa, 12 June 1969, Flint & Gómez, 1♀ (NMNH). Valle Nuevo, SE Constanza, c. 7,000 ft. [2135 m], August 1938, Darlington, 1♀ (MCZ). **Dajabón Province**: Río Massacre, Balneario Don Miguel, 7 km SW Dajabón, 40 m, 26 May 1973, D. and M. Davis, 4♀ (NMNH). **Elias Piña Province**: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 1♂, 2♀ (FSCA). **Puerto Plata Province**: Los Hidalgos, 4–5 June 1969, Flint & Gómez, 1♀ (NMNH).

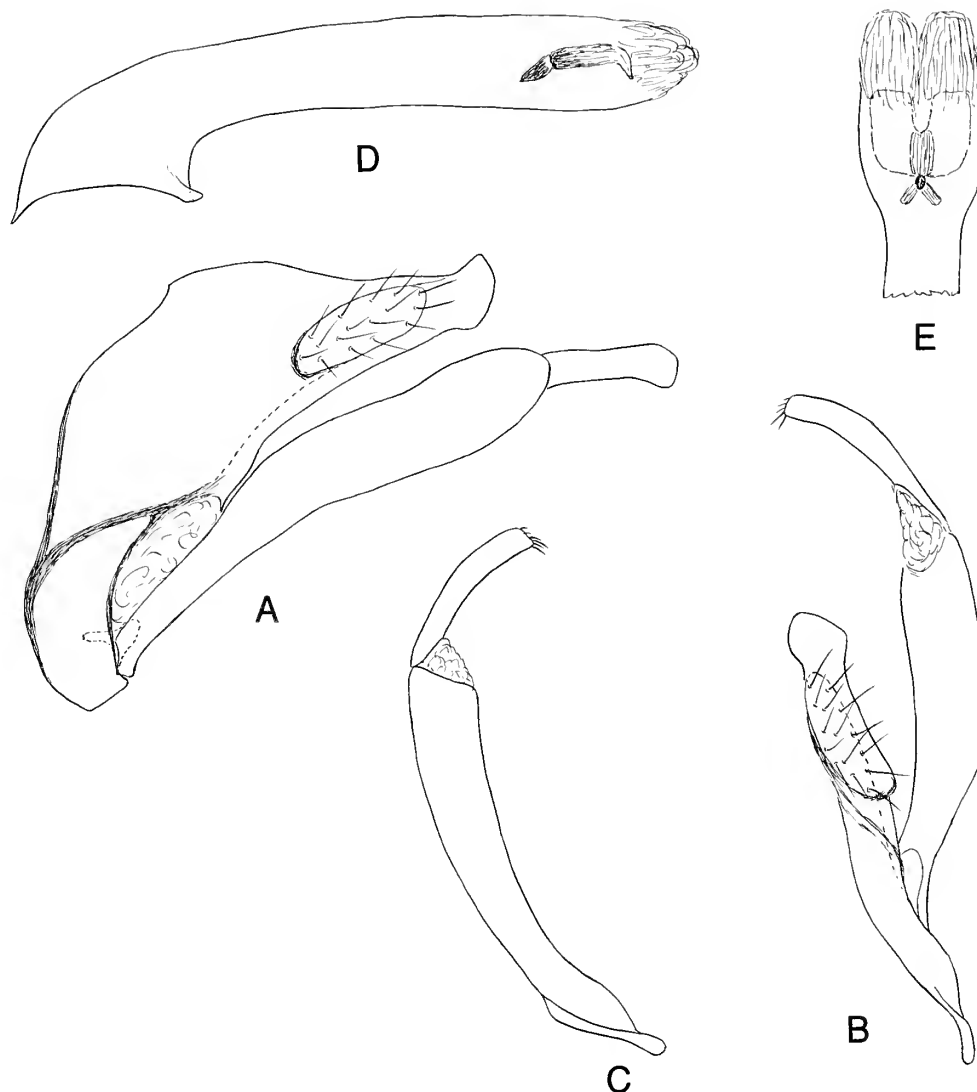


Fig. 14.—*Smicridea* (*S.*) *brunescens* new species, male genitalia: A, Lateral. B, Tenth tergum and inferior appendage, dorsal. C, Inferior appendage, posteroventral. D, Phallus, lateral. E, Tip of phallus, ventral.

Smicridea (*Smicridea*) *comma* Banks

Smicridea comma Banks, 1924:451. Flint, 1967:14, figs. 59, 60 [♂]; Kumanski, 1987:12, fig. 8 [♂, ♀, Haiti]; Botosaneanu, 1991a:133 [Haiti]; Botosaneanu, 1996:15 [Dominican Republic].

Originally described from Cuba where it is very frequent and abundant, it has been recorded recently from Haiti and the Dominican Republic. The species seems to be equally frequent and abundant on Hispaniola. It is recorded from Duarte, Monte Plata, Independencia, Pedernales and we here add Azua, Barahona, Dajabón, El Seibo, Hato Mayor, La Vega, Puerto Plata, San Cristóbal, and San Juan Provinces.

Material Examined.—**DOMINICAN REPUBLIC.** **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 43♂, 28♀ (CMNH); same, but 7 August

1990, 60 ♂♂ ♀♀ (CMNH). **Barahona Province:** Río Yaqui del Sud [sic.], 25 m from mouth, 18 September [1938?], Darlington, 1♀ (MCZ). Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, Flint, 1♂ (NMNH). 24 km E Barahona, 27 September 1985, Woodruff & Stange, 3♂, 10♀ (FSCA). **Dajabón Province:** 9 km S Loma de Cabrera, 19°21'N, 71°37'W, 620 m, 12 July 1992, Rawlins et al., 7♂, 8♀ (CMNH). Río Massacre, Balneario Don Miguel, 7 km SW Dajabón, 40 m, 26 May 1973, D. & M. Davis, 79♂, 40♀ (NMNH). **Elias Piña Province:** Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 3♂, 3♀ (FSCA). **El Seibo Province:** Río Quisibani, E El Seibo, 18°45.3'N, 68°55.7'W, 12 May 1995, Flint, 10♂, 5♀ (NMNH). Loma Cocuyo, 6 km N Pedro Sánchez, 18°55'N, 69°07'W, 475 m, 4 July 1992, Rawlins et al., 13♂, 20♀ (CMNH). Hotel Santa Cruz, 28 May 1985, Woodruff & Stange, 1♀ (FSCA). Río Chavón, 17 km SE El Seibo, 28 May 1985, Woodruff & Stange, 50 ♂♂ ♀♀ (FSCA). Pedro Sánchez, small stream, 10 June 1976, Woodruff, 50 ♂♂ ♀♀ (FSCA). **Hato Mayor Province:** Parque Los Haitises, E of Trepada, 12 km E El Valle, 18°59'N, 69°30'W, 145 m, 6 July 1995, Rawlins et al., 100 ♂♂ ♀♀ (CMNH). **Independencia Province:** Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March

1999, Flint, 2♂, 2♀ (NMNH). Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 15♂, 8♀ (NMNH). **La Altagracia Province:** 2 km E Nisibón, Río Nisibón, 12 June 1986, Woodruff & Stange, 100 ♂♂ ♀♀ (FSCA). Nisibón, "Papagallo", 16–19 June 1998, Woodruff & Freytag, 1♀ (FSCA); same, but 16–19 June 1999, Woodruff & Baranowski, 1♀ (FSCA). La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 50 ♂♂ ♀♀ (FSCA). **La Vega Province:** Jarabacoa, 3–4 June 1969, Flint & Gómez, 4♀ (NMNH). Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 4♂, 5♀ (NMNH); same, but 19–21 May 1995, 4♂, 5♀ (NMNH). Río Camú, 19 km NE Jarabacoa, 12 June 1969, Flint & Gómez, 21♂, 28♀ (NMNH). Bayacanes, 120 m, 24 July 1987, Rawlins & Davidson, 1♂, 2♀ (CMNH). **Monseñor Nouel Province:** Bonao, Hotel Jacaranda, 27–28 June 1988, Woodruff & Baranowski, 50 ♂♂ ♀♀ (FSCA); same, but 28–30 June 1999, 4♂, 8♀ (FSCA); same, but 18 April 2000, Woodruff & Henry, 50♂, 70♀ (FSCA). 12 km W Rt. 1 on Constanza Rd., 30 June 1999, Woodruff, 1♂ (FSCA). **Monte Cristi Province:** Monte Cristi, 4 June 1986, Miller & Stange, 10♂, 25♀ (FSCA). 3 km N Villa Elisa, 1 October 1985, Woodruff & Stange, 9♂, 7♀ (FSCA). **Monte Plata Province:** Bayaguana, 22 August–2 September 1991, Brown, 30 ♂♂ ♀♀ (FSCA). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 8♂, 5♀ (NMNH); same, but 18 March 1999, Flint, 47♂, 48♀ (NMNH); same, but 20 March 1999, 11♂, 22♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 148♂, 108♀ (CMNH). Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 4♂, 8♀ (NMNH). Km 15, N Cabo Rojo, 850 ft [260 m], 11 April 2000, Woodruff & Henry, 1♂, 1♀ (FSCA). 20.5 km N Cabo Rojo, 12 April 2000, Woodruff & Henry, 1♀ (FSCA). Km 21, N Cabo Rojo, 1200 ft [365 m], 1 July 1998, Woodruff & Baranowski, 8♂, 14♀ (FSCA). 23.5 km N Cabo Rojo, 18°06'N, 71°38'W, 540m, 20 July 1990, Rawlins et al., 1♂ (CMNH). K 24, N. Cabo Rojo, 3000 ft [915 m], 2 July 1998, Woodruff & Baranowski, 2♂ (FSCA); same, but 23 June 1999, 1♀ (FSCA). 5 km N Mercedes, 24 June 1999, Woodruff & Baranowski, 1♂, 3♀ (FSCA). **Peravia Province:** 8 km W Baní, 25 May 1985, Woodruff & Stange, 8♂, 7♀ (FSCA). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 5♂, 6♀ (NMNH). Los Hidalgos, 4–5 June 1969, Flint & Gómez, 24♂, 29♀ (NMNH). **San Cristóbal Province:** La Toma, July 1969, Maldonado, 1♂, 1♀ (NMNH); same, but N of San Cristóbal, 9–10 June 1969, Flint & Gómez, 17♂, 14♀ (NMNH). Hato Dumas, 21 October 1986, Woodruff & Frank, 50 ♂♂ ♀♀ (FSCA). La Trinidad, NE Sierra de Agua, 2 May 1978, Woodruff et al., 13♂, 11♀ (FSCA). **San Juan Province:** Presa de Sabaneta, 11 km WNW Hato Nuevo, 1 km SE Ingenito, 19°02'N, 71°18'W, 610 m, 31 August 1995, Rawlins et al., 1♀ (CMNH). Río Mijo, 20 May 1985, Woodruff & Stange, 11♂, 10♀ (FSCA); same, 22 May 1985, Woodruff & Nuñez, 30 ♂♂ ♀♀ (FSCA). 1 km off rd. to Vallejuelo at river, El Capá, 21 May 1985, Woodruff & Stange, 7♂, 11♀ (FSCA). **Santiago Province:** Santiago (NW Arroyo), 25 April 1978, Woodruff, 1♂ (FSCA).

Smicridea (Smicridea) banksi Flint
(Fig. 15)

Smicridea unicolor Banks, 1938:303, fig. 25 [♂; secondary junior homonym].

Smicridea banksi Flint, 1967:13, figs. 61–63 [new name for *S. unicolor* Banks 1938, lectotype ♂]. Botosaneanu, 1996:15 [Dominican Republic].

This species was originally described from the La Selle Range in Haiti and recently recorded from the adjacent Province of Pedernales in the Sierra de Baoruco. We give here new, more detailed figures of the male genitalia of the lectotype to help with the recognition of this and closely related species, and fully discuss them under *S. duarte* n. sp. The type series is now faded to a dark, reddish-brown, but a faint indication of a very narrow

white, transverse band is apparent on the forewing, but no opalescent hairs nor white apical fringe are evident. The coloration for this species recorded under *S. duarte* is from the fresh material here recorded.

The new series listed here were taken at the eastern end of the Cordillera Central whereas the types are from a southern range in Haiti. However, *S. duarte*, which varies very little, is known from the Sierra de Baoruco, the Cordillera Central and the Cordillera Septentrional. *Smicridea completa* was described from the coastal hills in the south central area and recorded now from the Central Cordillera and just inland of Pedernales near the Haitian border. Apparently all species have a widespread, but poorly known, distribution.

Material Examined.—HAITI. [Département de L'Ouest]: La Visite & vic., La Selle Range, 5–7000 ft [1525–2135 m], 16–23 September 1934, M. Bates, ♂ lectotype, 2♂, 1♀ paratypes (MCZ).

DOMINICAN REPUBLIC. **La Vega Province:** 15 km S Constanza, 3 Jun 1969, Flint and Gomez, 1♂ (NMNH). Convento, 12 km S Constanza, 6–13 Jun 1969, Flint and Gomez, 1♂, 2♀ (NMNH). **Monseñor Nouel Province:** nr. Jima [6.3 km W jct. Carretera Duarte and rt. 12], 19°01.2'N, 70°28.8'W, 670 m, 6 May 1995, Flint, 5♂ (NMNH, CMNH). La Vaca, 6km W Jayaco, 2 Jun 1969, Flint and Ortiz, 4♂ (NMNH).

Smicridea (Smicridea) completa Banks
(Fig. 16)

Smicridea completa Banks, 1941:398, fig. 25 [♂]. Flint, 1967:14, figs. 64, 65 [♂].

The lectotype of this species, here figured, is from Villa Altagracia, a region of low hills and now mostly transformed by agriculture. The abdomen of the female paratype has been cleared and compared with the cleared genitalia of the example from Constanza and a specimen from Río Mulito: all have been found to be in substantial agreement. The example from Constanza may well have been the one listed by Banks in his original description. It no longer carries any type indication as is usual with all examples in a type series from the MCZ. See the comments under *S. duarte* for distinctive characteristics of this species.

Material Examined.—DOMINICAN REPUBLIC. [La Vega Province]: Constanza, 3–4000 ft. [915–1220 m], August 1938, Darlington, 1♀ (MCZ). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 57♂, 35♀ (NMNH); same, but 18 March 1999, 95♂, 48♀ (NMNH, FSCA); same, but 20 March 1999, 44♂, 31♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 274♂, 86♀ (CMNH). Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 13♂ (NMNH). [San Cristobal Province]: Villa Altagracia, July 1938, Darlington, ♂ lectotype, 1♀ paratype (MCZ).

Smicridea (Smicridea) duarte
Flint and Sykora, new species
(Fig. 17)

This species is very closely related to *S. banksi* and *S. completa*. We give here the differences apparent to us

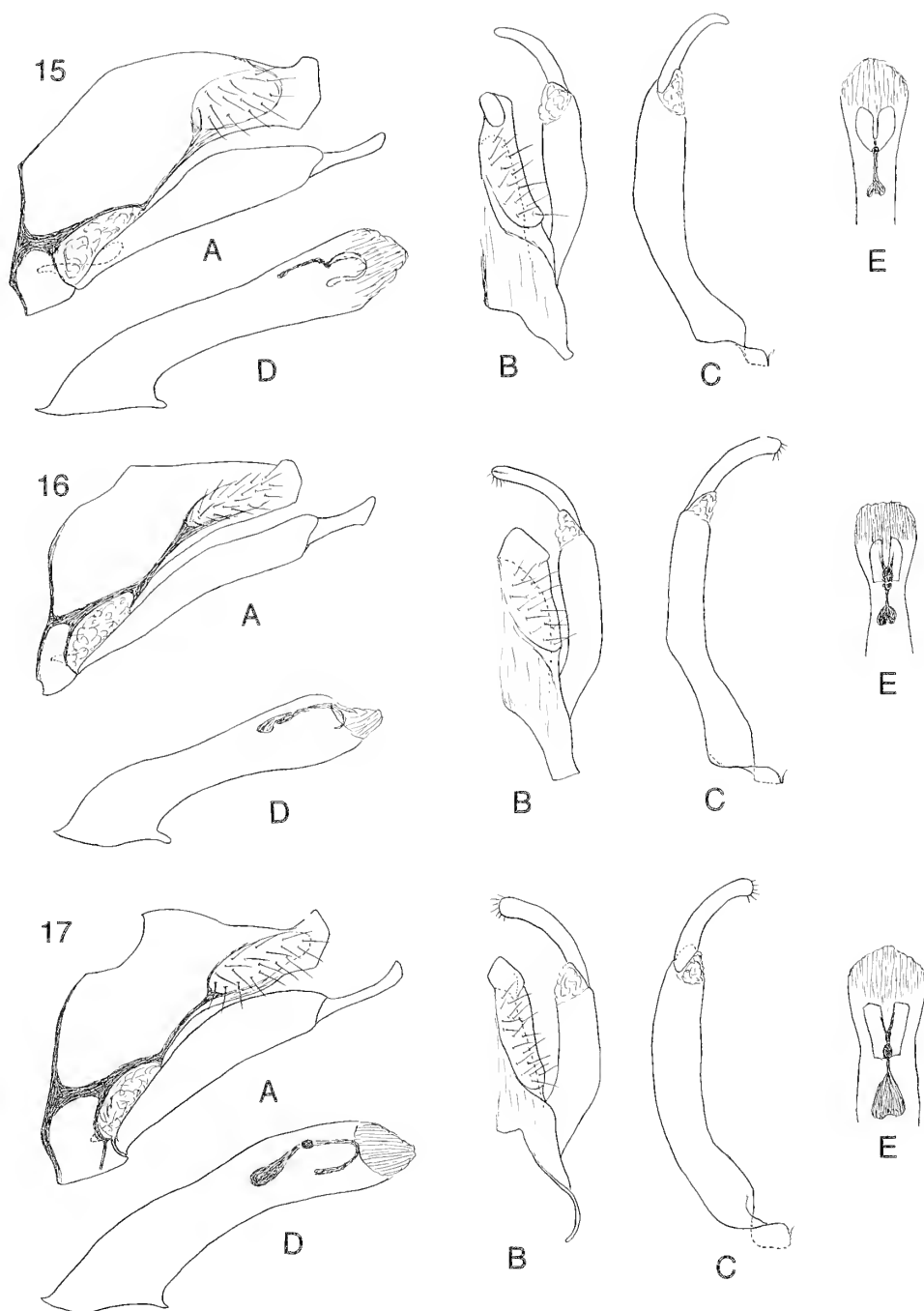


Fig. 15.—*Smicridea* (*S.*) *banksi* Flint, male genitalia: A, Lateral. B, Tenth tergum and inferior appendage, dorsal. C, Inferior appendage, posteroventral. D, Phallus, lateral. E, Tip of phallus, dorsal.

Fig. 16.—*Smicridea* (*S.*) *completa* Banks, male genitalia: A, Lateral. B, Tenth tergum and inferior appendage, dorsal. C, Inferior appendage, posteroventral. D, Phallus, lateral. E, Tip of phallus, dorsal.

Fig. 17.—*Smicridea* (*S.*) *duarte* new species, male genitalia: A, Lateral. B, Tenth tergum and inferior appendage, dorsal. C, Inferior appendage, posteroventral. D, Phallus, lateral. E, Tip of phallus, dorsal.

among the species of this complex. All three are basically fuscous with a narrow, transverse band of white hair at 3/4 of the forewing length. However, *S. banksi* has a broad, diffuse band of opalescent hair midway between the white

band and the wing base, and the apical fringe either dark or white. In *S. completa* the opalescent hairs cover the entire basal half of the forewing, and there is a second large area of purplish, opalescent hair between the white

band and the apex which has a white fringe. *Smicridea duarte* has three bands of opalescent hair, one at the forewing base, the second midway between the base and the white band and the last just apicad of the white band, the apex has a white fringe.

In the male genitalia the anterior margin of the ninth segment in *S. duarte* is deeply concave dorsally, barely so in *S. completa* and oblique and straight in *S. banksi*. The tip of the tenth tergite in dorsal aspect is very oblique and produced into a small lateral angle in *S. duarte*; is oblique and broad with a definite lateral angle in *S. completa*, and is barely oblique and produced into a dorsomesal knob in *S. banksi*. The lateral wart of the tenth tergite in lateral aspect in *S. duarte* and *S. completa* is at least three times as long as broad, but less than twice as long as broad in *S. banksi*. The basal segment of the inferior appendage in lateral aspect is inflated subapically in both *S. duarte* and *S. banksi*, but parallel-sided in *S. completa*. The apical segment of the inferior appendage in posteroventral aspect in *S. duarte* is rounded, in *S. completa* is more truncate, and in *S. banksi* tapers to a narrow, rounded point. The phallus seems to curve from the base into the stem in *S. banksi* and *S. completa*, but runs directly from base into stem in *S. duarte*. The phallotremal sclerite in *S. banksi* and *S. completa* has a relatively short expanded portion basally, but this expanded portion is much longer in *S. duarte*, extending almost to the apical "wings".

Adult Male.—Length of forewing, 5–5.5 mm. Color fuscous; midfemur with white hair, midtarsi stramineous; forewing fuscous, with narrow, transverse, white stripe at 3/4 length (not notably widened on costal margin), and three bands of opalescent hair, one at forewing base, second midway between base and white stripe, last just apicad of white band, apex with white fringe. Abdomen with four internal, reticulate sacs, each about 1.5 times as long as its segment. Genitalia: Ninth segment in lateral aspect with anterior margin vertical centrally, deeply concave dorsally. Tenth tergum with tip in lateral aspect produced dorsad, oblique in dorsal aspect with small lateral angle; lateral wart about 3 times as long as broad, anterior angle pointed in lateral aspect. Inferior appendage with basal segment straight, slightly inflated apically in lateral aspect, with slight basomesal angle in ventral aspect; apical segment elongate, parallel-sided, apex rounded with small tuft of setae. Phallus tubular, angled posteriad directly from base; phallotremal sclerites elongate, ribbon-like in lateral aspect; with broad apico-lateral "wings" in dorsal aspect and with elongate anteromesal sclerite gradually widening anteriorly.

Female.—Length of forewing, 5.5–6 mm. Color fuscous; marked as in male. Genitalia: Ninth segment broad ventrally. Clasper groove slightly impressed, curved, with rugosities as it enters receptacle; receptacle triangular in outline, anterior margin open, at postero-ventral angle of segment.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC, [La Vega Province]:** Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, O.S. Flint (NMNH). Paratypes; same data 5♂, 5♀ (NMNH, CMNH); same, but 19–21 May 1995, 2♂, 4♀ (NMNH); same, but 14–17 May 1998, W.N. Mathis, 2♂, 1♀ (NMNH). 5 km S Jarabacoa, 19°05.8'N, 70°36.5'W, 640 m, 8–20 May 1995, W.N. Mathis, 1♀ (NMNH). Salto Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, O.S. Flint, 3♂, 2♀ (NMNH). La Palma, 12 km E El Río, 2–13 Jun 1969, Flint & Gomez, 1♂ (NMNH). **Baoruco Province:** Sierra de Neiba, Los Guineos on upper Río Colorado, 18°35'N, 71°11'W, 630 m, 11–12 August 1990, Rawlins & Thompson, 1♀ (CMNH). **Barahona Province:** San Rafael, 8.3 km S Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 15 May 1995, O.S. Flint, 1♂ (NMNH); same, but 22 March 1999, 2♀ (NMNH). Ojeda, 17°58.2'N, 71°10.6'W, 22 March 1999, W.N. Mathis, 4♂, 1♀ (NMNH). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 3♂, 9♀ (CMNH). Confluence Río Nizaito and Río Cortico, 9.2 km NW Paraiso, 18°03'N, 71°12'W, 230 m, 9–10 August 1990, Rawlins & Thompson, 1♀ (CMNH). **Elias Piña Province:** Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 2♂, 3♀ (FSCA). 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. and M. Davis, 1♂, 1♀ (NMNH). **Independencia Province:** Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 6♂, 9♀ (NMNH). Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, O.S. Flint, 10♂, 3♀ (NMNH). **Pedernales Province:** Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 3♀ (NMNH). **Peravia Province:** 10 km E San José de Ocoa, 18°35'N, 70°25.6'W, 21 May 1998, W.N. Mathis, 24♂ (NMNH). **Puerto Plata Province:** Sonador, 19°35.9'N, 70°36.2'W, 440 m, 18 May 1995, O.S. Flint, 6♂ (NMNH, CMNH); same, but W.N. Mathis, 1♂ (NMNH).

Other: **HAYTI** [sic.], Chipman, Holland Collection [no further data], 1♂ (CMNH).

Family Hydroptilidae Genus *Alisotrichia* Flint

This genus of exclusively New World distribution is found from the southwestern United States south through Central America into northern South America and south along the Andes at least to Peru. It is very diverse on the Antillean islands, each of the Greater Antillean islands having three to ten species (with one fossil known from Dominican amber, Wells and Wichard, 1989) and the Lesser Antillean islands one or two apiece. The immature stages of several species have been described (Bowles et al., 1999; Flint, 1964, 1970). All the larvae so far found have been taken in madicolous or hygropetric situations. The adults are quite active, running on rocks in the bright sun, but may also come to light at night.

Alisotrichia aglae Botosaneanu

Alisotrichia aglae Botosaneanu, 1991a:118, figs. 18–21 [♂].

The species was described from a single site in Haiti and no further records have been presented. It is here recorded from several sites in the Provinces of Barahona and Independencia.

Material Examined.—**DOMINICAN REPUBLIC, Barahona Province:** Larimar Mine, nr. Filipinas, 26 June–7 July 1992, Woodruff & Skelley, 1♂ (FSCA). San Rafael, 8.3 km S Baoruco, 18°01.9'N,

71°08.4'W, 30 m, 22 March 1999, Flint, 1♂ (NMNH). **Independencia Province:** Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, O.S. Flint, 7♂ (NMNH, CMNH).

Alisotrichia aquaecadentis Botosaneanu

Alisotrichia aquaecadentis Botosaneanu, 1991a:116, figs. 7–11 [♂, ♀].

As is the case with the preceding species, this species was known only from a single site in Haiti. It is here recorded from the Province of Independencia, the first record from the Dominican Republic.

Material Examined.—**DOMINICAN REPUBLIC. Independencia Province:** Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 5♂ (NMNH, CMNH).

Alisotrichia arcana Botosaneanu

Alisotrichia arcana Botosaneanu, 1991a:124, figs. 29–36 [♂].

Another species described from a single site in Haiti, this one has not been recollected.

Alisotrichia bisetosa Flint and Sykora, new species
(Fig. 18)

This species and *A. circumata* from Puerto Rico appear to be closely related. Both have a strongly modified antennal scape and similar ventral structure of the ninth-tenth male genital segments. From *A. circumata*, *A. bisetosa* may be easily recognized by the modified male maxillary palpi, the structure of the eighth sternum with its second setiferous tubercle, and very broad, complex phallus.

As frequently happens in this genus, the true homologies of structures in the male genital capsule are incomprehensible. Thus homologies are only suggested and the differentiation of phallic and tenth tergal structures is unresolved.

Adult Male.—Length of forewing 2 mm. Color fuscous marked with silvery white hair on antenna, head, and mesothorax; forewing fuscous with white hair along anterior margin and in several obliquely transverse bands. Ocelli two. Scape greatly enlarged, covering face anteriorly, contiguous mesally, with ventromesal, cylindrical lobe, concave internally with internal surface “corrugate”; 15 segments beyond scape, basal segment of which twice as long as broad, other segments slightly broader than long, apical segment elongate, bearing apical nipple. Maxillary palpus with fifth segment tapering, conical; fourth segment flattened with enlarged setae laterally; third segment short, produced laterad and bearing tuft of large setae directed laterad; basal segments very short and hidden in hair. Spurs 0.2, 4; hind tibia with elongate hair fringe; basal segment of hind tarsus longer than remaining segments, bearing tuft of very long setae. Seventh sternum with very small sclerotized process apicomeresally. Genitalia: Eighth sternum bilobate, apically lacking enlarged setae; posterior margin dorsolaterally

with large lobe bearing dorsally very large, black seta; dorsal margin with small papilla bearing apically large, pale seta. Terminal complex (ninth and tenth segments and phallus) with long, slender lateral rods (from ninth segment?) reaching to seventh segment; dorsally with usual pair of parenthesis-like dark marks (on tenth segment?) with apices curving laterad and ventrad; in lateral aspect with apically liplike structure, basally developed in coiled manner; phallus basally flared, reduced to narrow neck, enlarged apically with complex internal structure (part of which may be associated tenth tergal structures).

Female.—Not associated with certainty.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. Independencia Province:** Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, O.S. Flint (NMNH). Paratypes: Same data, 5♂ (NMNH). **Barahona Province:** Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, O.S. Flint, 2♂ (NMNH). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 2♂ (CMNH). **Independencia Province:** La Descubierta, 3 August 1983, R.E. Woodruff, 1♂ (FSCA). **La Vega Province:** Constanza, 27 April 1978, Woodruff & Fairchild, 9♂, 2♀ (FSCA, NMNH).

Alisotrichia euphrosyne Botosaneanu

Alisotrichia euphrosyne Botosaneanu, 1991a:118, figs. 22–24 [♂].

One more species described from a single site in Haiti, it is now recorded from a site in Pedernales Province, Dominican Republic.

Material Examined.—**DOMINICAN REPUBLIC. Pedernales Province:** Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 1♂, 2♀ (NMNH).

Alisotrichia hiruopsis aitija Botosaneanu

Alisotrichia hiruopsis aitija Botosaneanu, 1995:22, figs 1—4 [♂].

The nomotypical subspecies is common on hygropteric situations in Puerto Rico. This subspecies of *A. hiruopsis* was described from the Province of Duarte. It has now been taken also in the Provinces of La Vega, Monseñor Noel and Peravia.

Material Examined.—**DOMINICAN REPUBLIC. La Vega Province:** Salto Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 9 May 1995, Flint, 66♂, 8♀ (NMNH, CMNH). 5 km W Manabao, Finca Eliado Fernandez “Paso la Perra”, along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 1♀ (FSCA). **Monseñor Noel Province:** 20 km W Bonao, Hydroelectric Plant, Río Blanco, 600 m, 13 May 2001, Woodruff & Nuñez, 5♂, 3♀ (FSCA). **Peravia Province:** 10 km E San José de Ocoa, 18°35'N, 70°25.6'W, 21 May 1998, Mathis, 5♂ (NMNH).

Alisotrichia hispaniolina Botosaneanu

Alisotrichia hispaniolina Botosaneanu, 1991a:116, figs 12–17 [♂, ♀]. Botosaneanu, 1995:23 [tentative record of a ♀].

A species known from a number of localities in Haiti, it was tentatively recorded from the Province of Pedernales in the Dominican Republic. We now confirm this

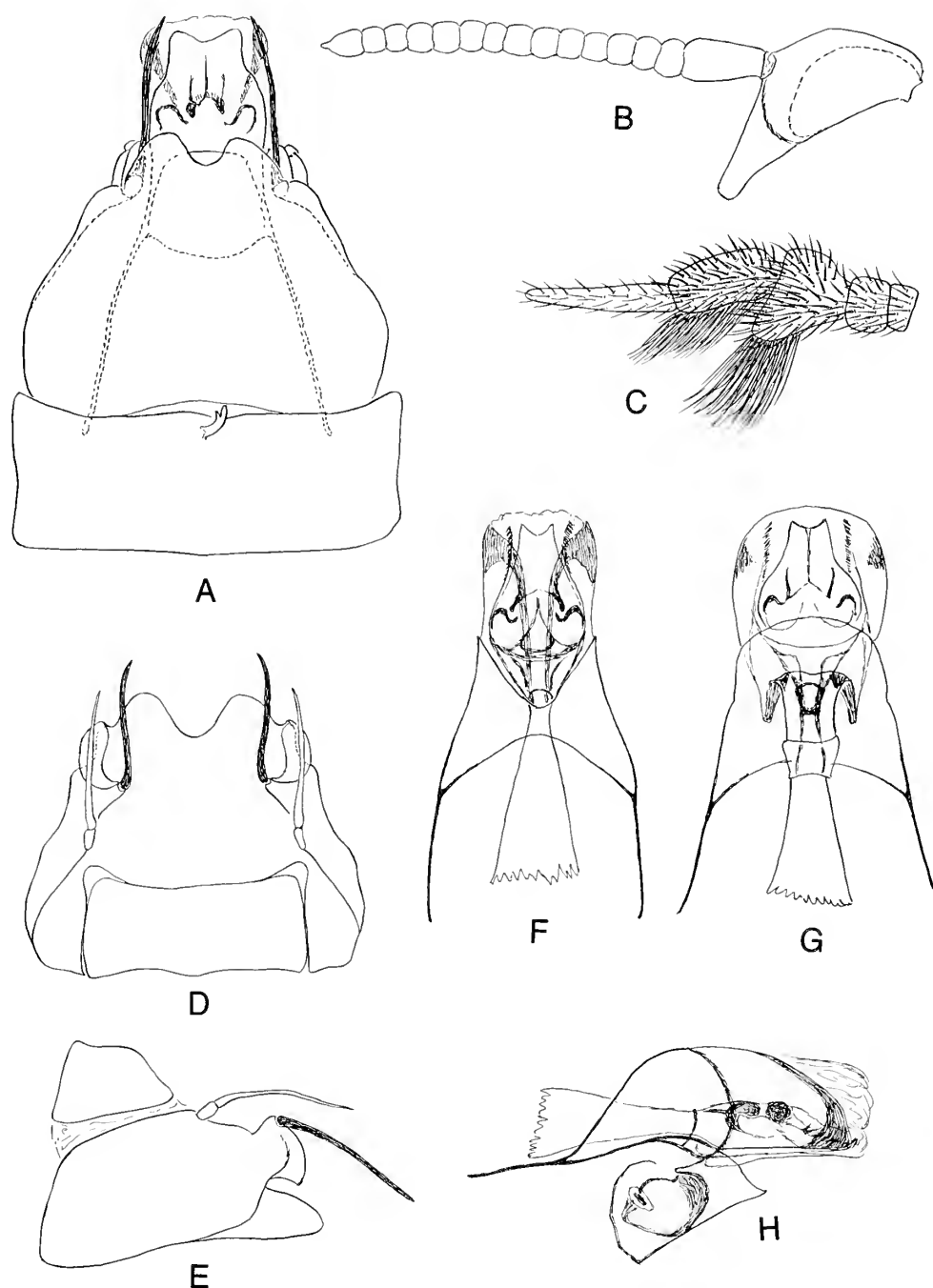


Fig. 18.—*Alisotrichia bisetosa* new species, male genitalia A. Ventral. B. Antenna, lateral. C. Maxillary palpus, lateral. D. Eighth segment, dorsal. E. Eighth segment, lateral. F. Ninth and tenth terga and phallus, dorsal. G. Ninth and tenth terga and phallus, ventral. H. Ninth and tenth terga and phallus, lateral.

provincial record and add the provinces of Azua, Barahona, and Independencia.

Material Examined.—DOMINICAN REPUBLIC. **Azua Province**: Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 67♂, 8♀ (CMNH, NMNH); same, but 7 August 1990, 4♂, 2♀ (CMNH). **Sec. Canoa**, Mirador de la Presa, Yaqui del Sur, 30 September 1978, Woodruff, 1♀ (FSCA). **Barahona Province**: Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, Flint & Mathis, 69♂, 65♀ (NMNH). Río Nizaito, 6

km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 4♂, 8♀ (CMNH). Confluence Río Nizaito and Río Cortico, 9.2 km NW Paraiso, 18°03'N, 71°12'W, 230 m, 9–10 August 1990, Rawlins & Thompson, 6♂, 1♀ (CMNH). **Independencia Province**: Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 3♂ (NMNH). **Pedernales Province**: 20.5 km N Cabo Rojo, 12 April 2000, Woodruff & Henry, 10♂, 14♀ (FSCA, NMNH). N Cabo Rojo, km 21, 1200 ft. (365 m), 19 June 1976, Woodruff, 1♀ (FSCA); same, but 1 July 1998, Woodruff & Baranowski, 1♂, 3♀ (FSCA); same, but km 24, 3000 ft (915 m), 2 July 1998, 2♂, 1♀ (FSCA).

Alisotrichia thalia Botosaneanu

Alisotrichia thalia Botosaneanu, 1991a:120, figs 25–28 [♂].

Previously known from only one site in Haiti, we here record it from a site in the Province of Barahona in the Dominican Republic.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** San Rafael, 8.3 km S of Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 11 May 1995, Flint, 1♂, 3♀ (NMNH).

Alisotrichia woodruffi Flint and Sykora, **new species** (Fig. 19)

Although the male genitalia of this species are quite typical of many species in the genus, particularly the *A. orophila* Group, the combination of characters of the maxillary palpi, antennae, and eighth sternum render this species unique. The greatly broadened and cupped antennal flagellum greatly surpasses this condition seen in the Jamaican *A. tenuivirga* Botosaneanu or *A. ultima* n. sp., the only other Greater Antillean species with broadened flagellar segments and processes with long setae dorsally from the eighth sternum. *Alisotrichia hindopsis* has antennae identically formed as *A. woodruffi*, but lacks the eighth sternal structures. Many species have modified male maxillary palpi, but generally the third not the fourth segment, as is the case in *A. tenuivirga* and *A. woodruffi*. However, *A. woodruffi* is unique among described Greater Antillean species in having a totally unornamented posterior margin of the eighth sternum. Details of the ninth and tenth segments and phallic complex also offer other distinctive characteristics, especially the hooked subgenital process.

Adult Male.—Length of forewing 2 mm. Color fuscous in alcohol. Ocelli 2. Scape greatly enlarged, covering face anteriorly, contiguous mesally, with broad ventral lobe bearing brush of long setae anteroventrally, concave dorsally with internal corrugate sac; 15 segments beyond scape, basal segment of which longer than broad, segments 5–8, especially, much broader than long, concave mesally, inner and outer faces covered with short, spatulate setae, apical segment elongate, bearing apical nipple. Maxillary palpus with fifth segment tapering, conical; fourth segment flattened and broadened apicolaterally, third segment elongate, terete; third and fourth segments covered with elongate, spatulate setae, especially on outer face; basal segments very short and hidden in hair. Spurs 0,2,4; hind tibia and tarsus distinctly hairy. Seventh sternum with very small apicomesal point. Genitalia: Eighth sternum bilobate apically, lacking enlarged setae; anterodorsally with long, slender lobe bearing very large, black seta. Terminal complex (ninth and tenth segments and phallus) with long, slender lateral rods (from ninth segment?) reaching to seventh segment; dorsally with usual pair of parenthesis-like dark marks (on tenth segment?) with apices curving laterad and ventrad; in lateral aspect, with structure produced apically and

basally into liplike process; with subgenital process, hooked ventrad in lateral aspect, crescentic in ventral aspect; phallus basally flared, reduced to narrow neck, enlarged at midlength with curved internal sclerite in lateral aspect, produced into slender apical plates, appearing as two parallel lines in dorsal aspect.

Female.—Not securely associated.

Type Material.—Holotype, male: DOMINICAN REPUBLIC. **Monseñor Nouel Province** [not La Vega as labelled]: 6km [not mi. as labelled] NW Rt.1 on road to Constanza, 27 June 1998, Woodruff & Baranowski (FSCA). Paratypes: Same data, 1♂ (NMNH).

Alisotrichia ultima Flint and Sykora, **new species** (Fig. 20)

This recently discovered, distinctive species appears to be related to *A. thalia* on the basis of the ornamentation of the eighth sternum, but the modifications of the head and legs are more a melange of those of *A. woodruffi* and *A. bisetosa*. The antennal structure is much like that of *A. woodruffi* but the scape has different modifications, the pedicel is simply cylindrical and the flattened segments are not so broad (actually much like those of *A. hindopsis* Flint 1964, Fig. 12D). The maxillary palpi are almost exactly like those of *A. bisetosa* (Fig. 18C). The hair tufts of the hind legs are like those of *A. bisetosa*, but there are also hair tufts on the midtibia. The apicolateral, pointed projection of the eighth sternum is much longer than in *A. thalia* and it is denticulate along the dorsal margin; the large seta this projection bears is identical in the two species. Unfortunately the internal structure of the ninth and tenth segments and the phallus is very faint and obscure in the type, although what can be discerned in lateral aspect looks much like that shown for *A. woodruffi*.

Adult Male.—Length of forewing 2 mm. Color fuscous in alcohol. Ocelli 2. Scape greatly enlarged, covering face anteriorly, contiguous mesally, and covered internally with short, scale-like setae, externally and especially ventrally with elongate, spatulate setae; pedicel elongate, cylindrical; 15 flagellar segments, segments 3–10, especially, much broader than long, concave mesally, inner and outer faces covered with short, spatulate setae, apical segment elongate, bearing apical nipple. Maxillary palpus with fifth segment tapering, conical; fourth segment flattened and broadened; third segment short, produced laterad and bearing tuft of large setae directed laterad; basal segments very short and hidden in hair. Spurs 0,2,4; midtibia with two very long hair brushes, one basally other apically; hindtibia apically and basal tarsal segment with long hair brushes. Seventh sternum with very small apicomesal point. Genitalia: Eighth sternum with posterolateral angle produced into elongate, pointed process curved mesad and bearing row of six small denticles dorsally, subapically bearing enlarged seta from venter; anterodorsally with long, slender lobe bearing very large, black seta. Terminal complex (ninth and tenth segments and phallus) with long, slender anterolateral

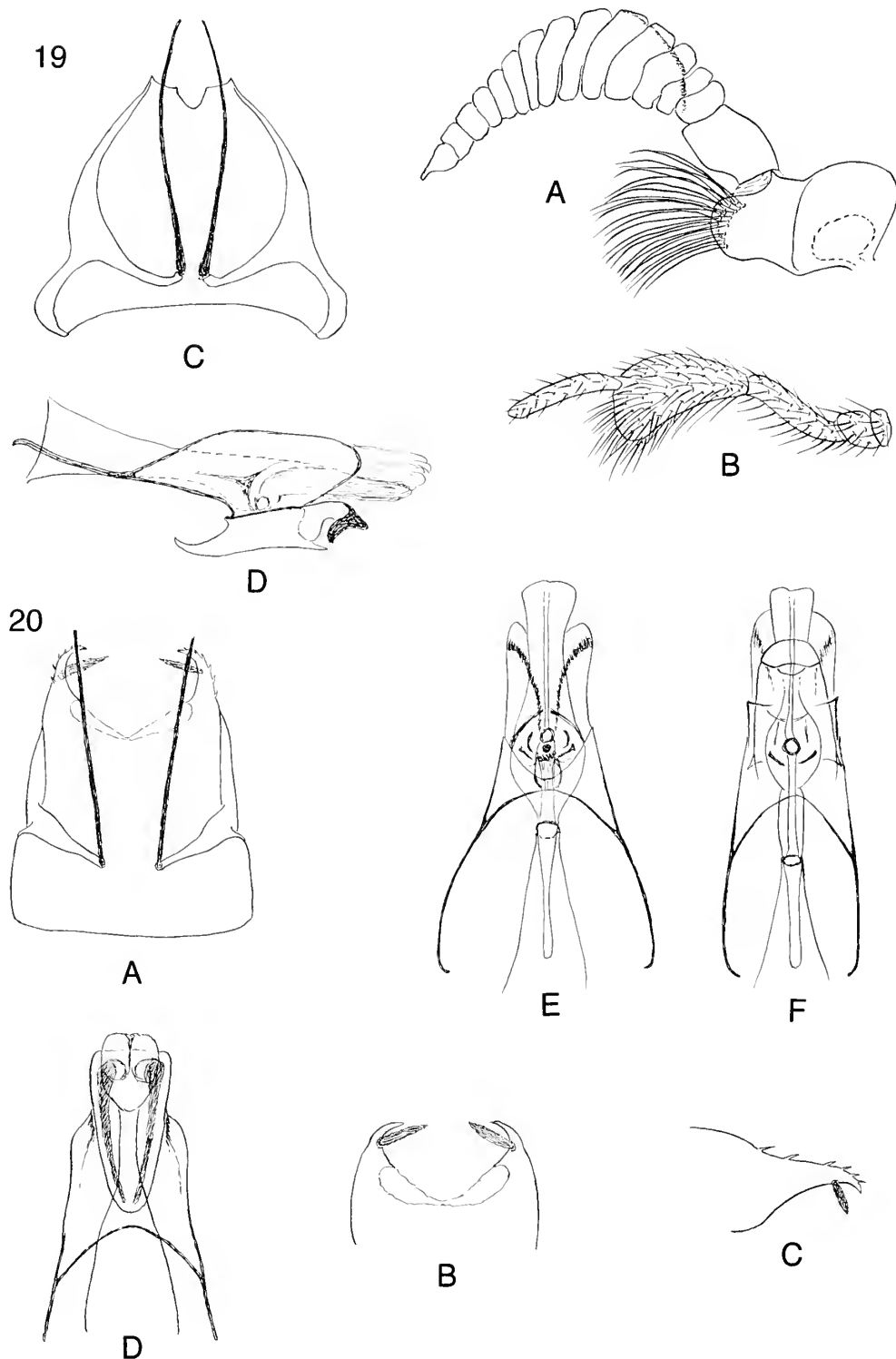


Fig. 19.—*Alisotrichia woodruffi* new species, male genitalia: A. Antenna, lateral. B. Maxillary palpus, lateral. C. Eighth sternum, dorsal. D. Ninth and tenth terga and phallus, lateral. E. Ninth and tenth terga and phallus, dorsal. F. Ninth and tenth terga and phallus, ventral.

Fig. 20.—*Alisotrichia ultima* new species, male genitalia: A. Eighth sternum, dorsal. B. Apex of eighth sternum, ventral. C. Apex of eighth sternum, lateral. D. Ninth and tenth terga and phallus, dorsal.

rods (from ninth segment?) reaching to seventh segment; dorsally with usual pair of parenthesis-like dark marks (on tenth segment?) with apices slightly enlarged; in lateral aspect, with a ventral structure produced apicad and basad into liplike process; with subgenital process, hooked ventrad in lateral aspect, crescentic in ventral aspect; phallus basally flared, reduced to narrow neck, enlarged before apex which is rounded and divided into elliptical, rounded hemispheres.

Female.—Unknown.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, J. Rawlins, C. Young, S. Thompson, & R. Davidson (CMNH).

Genus *Hydroptila* Dalman

Hydroptila is a genus found in all regions of the world, with a very large number of species in both temperate and tropical areas. The larvae have been described a number of times (Nielsen, 1948; Wiggins, 1996). They make purse shaped cases constructed of either plant material or sand grains. They generally feed on filamentous algae by piercing the cells, but may also ingest other types of algae.

Hydroptila ditalea Flint

Hydroptila ditalea Flint, 1968a:46 [♂, ♀]. Botosaneanu, 1995:27 [Dominican Republic].

Originally described from Jamaica, the species has been recorded from Mexico, Ecuador and Peru as well as the Dominican Republic, where it was known from the provinces of Duarte, Independencia, La Vega, Monte Plata, and Pedernales. We add the provinces of Azua, Barahona, Dajabón, Elías Piña, El Seibo, La Altagracia, La Romana, Monseñor Nouel, Puerto Plata, San Cristóbal, and San Juan.

Material Examined.—**DOMINICAN REPUBLIC. Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 2♀ (CMNH); same, but 7 August 1990, 5♀ (CMNH). Sec. Canoa, Mirador de la Presa, Yaqui del Sur, 30 September 1978, Woodruff, 2♂ (FSCA). **Barahona Province:** 24 km E Barahona, 27 September 1985, Woodruff & Stange, 1♀ (FSCA). **Dajabón Province:** Río Massacre, Balneario El Salto, Loma de Cabrera, 222 m, 21–25 May 1973, D. & M. Davis, 2♀ (NMNH). **Elías Piña Province:** Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 23♂, 15♀ (FSCA). **El Seibo Province:** Río Quisibani, E El Seibo, 18°45.3'N, 68°55.7'W, 12 May 1995, Flint, 6♂, 57♀ (NMNH). Pedro Sanchez, small stream, 10 June 1976, Woodruff, 10♂, 46♀ (FSCA). **Independencia Province:** La Descubierta, 3 August 1983, Woodruff, 2♂, 1♀ (FSCA). Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 2♂, 6♀ (NMNH). Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 5♀ (NMNH). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 3♂, 9♀ (FSCA). 2 km E Nisibón, Río Nisibón, 12 June 1986, Woodruff & Stange, 2♀ (FSCA). **La Romana Province:** La Romana, 16 September 1976, Folch, 2♀ (FSCA). **La Vega Province:** Río Baiguete, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 12♂, 62♀ (NMNH); same, but 19–21 May 1995, 10♂, 46♀ (NMNH). Río Camú, 19 km NE Jarabacoa, 12 June 1969, Flint & Gómez, 1♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°0.9'N, 70°33.5'W,

980 m, 7 May 1995, Flint, 1♀ (NMNH). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 2♂ (FSCA). **Monseñor Nouel Province:** Hotel Jacaranda, Bonao, 27–28 June 1998, Woodruff & Baranowski, 1♂, 2♀ (FSCA); same, but 18 April 2000, Woodruff & Henry, 1♂, 24♀ (FSCA). **Monte Plata Province:** Bayaguana, 22 August–2 September 1991, Brown, 2♀ (FSCA). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 5♂, 6♀ (NMNH); same, but 18 March 1999, Flint, 1♂, 2♀ (NMNH). Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 1♀ (NMNH). 20.5 km N Cabo Rojo, 12 April 2000, Woodruff & Henry, 1♀ (FSCA). N Cabo Rojo, km. 21, 1200 ft. [365 m], 1 July 1998, Woodruff & Baranowski, 4♀ (FSCA); same, but km. 24, 3000 ft (915 m), 2 July 1998, 1♀ (FSCA). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 21♀ (NMNH). Los Hidalgos, 4–5 June 1969, Flint & Gómez, 2♀ (NMNH). **San Cristóbal Province:** La Trinidad, NE Sierra de Agua, 2 May 1978, Woodruff et al., 1♀ (FSCA). **San Juan Province:** at river, 1 km off rd. to Vallejuelo, El Capá, 21 May 1985, Woodruff et al., 5♀ (FSCA). Río Mijo, 22 May 1985, Woodruff et al., 1♀ (FSCA).

Hydroptila dominicana Botosaneanu

Hydroptila dominicana Botosaneanu, 1995:27 [♂, ♀].

Originally described from the Dominican Republic, where it was recorded from the provinces of La Vega and Independencia. We add the provinces of Azua, Elías Piña, Pedernales, Puerto Plata, and San Juan. In addition, specimens have been taken in the Province of Cienfuegos in Cuba by Flint.

Material Examined.—**DOMINICAN REPUBLIC. Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 11♂, 33♀ (CMNH); same, but 7 August 1990, 2♂ (CMNH). **Elías Piña Province:** Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 3♂, 55♀ (FSCA). **Independencia Province:** Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 11♂, 54♀ (NMNH). **La Vega Province:** Río Baiguete, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 20♂, 69♀ (NMNH); same, but 19–21 May 1995, 1♀ (NMNH). Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 3♂, 6♀ (NMNH). Constanza, 2–6 June 1969, Flint & Gómez, 7♂, 4♀ (NMNH). El Convento, 12 km SE Constanza, 2–6 June 1969, Flint & Gómez, 1♂; same, but 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 3♂, 168♀ (NMNH). 11.5 km S. of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, Flint, 2♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°0.9'N, 70°33.5'W, 980 m, 7 May 1995, Flint, 1♂, 3♀ (NMNH). La Cienega de Manabao, Park Headquarters, 20–21 April 2000, Woodruff & Henry, 5♀ (FSCA). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 1♀ (FSCA). **Pedernales Province:** Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 1♀ (NMNH). 20.5 km N Cabo Rojo, 12 April 2000, Woodruff & Henry, 5♀ (FSCA). **Puerto Plata Province:** Los Hidalgos, 4–5 June 1969, Flint & Gómez, 1♂, 2♀ (NMNH). **San Juan Province:** at river, 1 km off rd. to Vallejuelo, El Capá, 21 May 1985, Woodruff et al., 4♀ (FSCA). Río Mijo, 22 May 1985, Woodruff et al., 1♀ (FSCA).

Hydroptila medinae Flint

Hydroptila medinae Flint, 1964:54 [♂, ♀]. Botosaneanu, 1991a:130 [Haiti].

The species was described originally from Puerto Rico and has since been recorded from Cuba and Haiti. These

records from the Provinces of El Seibo, La Altagracia, Pedernales, and Puerto Plata are the first from the Dominican Republic.

Material Examined.—**DOMINICAN REPUBLIC.** **El Seibo Province:** Río Quisibani, E. El Seibo, 18°45.3'N, 68°55.7'W, 12 May 1995, Flint, 11♂, 13♀ (NMNH). Pedro Sanchez, small stream, 10 June 1976, Woodruff, 3♂, 8♀ (FSCA). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 5♂, 1♀ (FSCA). **Pedernales Province:** N. Cabo Rojo, km. 21, 1200 ft (365 m), 19 June 1976, Woodruff, 1♀ (FSCA). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 14♀ (NMNH).

Genus *Leucotrichia* Mosely

The genus *Leucotrichia* is exclusively New World in distribution, being known from southern Canada south to Brazil. All the Greater Antillean islands support at least one species with a species known from Dominican amber (Wells and Wichard, 1989). A female, doubtfully belonging to this genus, is recorded from Martinique but otherwise the genus is known only on Grenada and south. The immature stages have been described a number of times (Flint, 1964, 1970; Wiggins, 1996). They live under a silken cover with an opening at both ends from which they extend the head and thorax to graze on surrounding periphyton.

Leucotrichia gomezi Flint

Leucotrichia gomezi Flint, 1970:7 [♂, larva, case].

This species was described from examples taken in central La Vega Province. No new material has been found.

Leucotrichia tubifex Flint

Leucotrichia tubifex Flint, 1964:44 [♂, ♀, larva, pupa, case, Puerto Rico]. Flint, 1968a:44 [Jamaica, ♂, ♀, larva, pupa, case]; Flint, 1970:7 [Dominican Republic, ♂, larva, case]; Botosaneanu, 1991a:116 [Haiti]; Botosaneanu, 1995:22 [Dominican Republic]; Botosaneanu & Bolland, 1997:71 [♀, parasitic mite].

Originally described from Puerto Rico, the species has subsequently been recorded from Jamaica, Haiti, and the Dominican Republic. In the Dominican Republic, it has been recorded only from the Province of La Vega; we here add the Provinces of Azua, Dajabón, Elías Piña, and El Seibo.

Material Examined.—**DOMINICAN REPUBLIC.** **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 1♂ (CMNH). **Dajabón Province:** 9 km S Loma de Cabrera, 19°21'N, 71°37'W, 620 m, 12 July 1992, Rawlins et al., 2♂, 1♀ (CMNH). **Elías Piña Province:** 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 1♂ (NMNH). **El Seibo Province:** Pedro Sanchez, small stream, 10 June 1976, Woodruff, 2♂, 1♀ (FSCA). **La Vega Province:** Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 3♂, 5♀ (NMNH); same, but 8–21 May 1995, Mathis, 2♀ (NMNH). Salto Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 1♂ (NMNH). La Cienega, nr. Manabao, 19°03.9'N, 70°51.8'W, 1050 m, 28 March 1999, Mathis, 1♂ (NMNH). 5 km W Manabao, Finca Eliado Fernandez "Paso

la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 3♂, 1♀ (FSCA).

Genus *Metrichia* Ross

This genus of exclusively New World distribution, is found from the southwestern United States, south through Mexico and Central America to Chile and including both the Greater and Lesser Antilles. The genus is quite speciose, with nearly 60 species described, many of which seem to be of very narrow distribution.

Larvae of several species have been described (Flint, 1964; Wiggins, 1996). They construct flattened, purse-shaped cases of silk and plant fragments, some species even add two "chimneys" to the dorsal margin (Botosaneanu and Flint, 1982).

Metrichia cafetalera Botosaneanu

Metrichia cafetalera Botosaneanu, 1980:110 [♂, Cuba]. Botosaneanu, 1995:26 [♂, ♀, Dominican Republic].

The species was originally described from the Province of Las Villas in Cuba and subsequently recorded from the Province of La Vega in the Dominican Republic. We have an additional collection from the Province of Peravia.

Material Examined.—**DOMINICAN REPUBLIC.** **Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°39'N, 70°36'W, 1880 m, cloud forest on river, 5–6 August 1990, Rawlins & Thompson, 15♂ (CMNH, NMNH). [**La Vega Province:** Convento, 12 km S Constanza, 6–13 June 1969, Flint & Gómez, 20♂, 59♀ (NMNH, CMNH, FSCA).

Metrichia fontismoreani (Botosaneanu)

Ochrotichia (*Metrichia*) *fontismoreani* Botosaneanu, 1991a:125 [♂, ♀, Haiti].

Metrichia fontismoreani (Botosaneanu): Botosaneanu, 1995:27 [♂ abdomen, ♀, Dominican Republic].

Another species described from Haiti, this one has been recorded from the provinces of La Vega, Duarte, and Independencia in the Dominican Republic. New material adds the provinces of Barahona and Monseñor Nouel to the distribution.

Material Examined.—**DOMINICAN REPUBLIC.** **Barahona Province:** San Rafael, 8.3 km S Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 22 March 1999, Flint, 13♂, 1♀ (NMNH). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins & Thompson, 2♂ (CMNH). **Independencia Province:** La Descubierta, 0 m, 18°34.1'N, 71°43.8'W, 25 March 1999, Flint, 1♂ (NMNH). **La Vega Province:** Salto Baiguate, nr. Jarabacoa, 19°05.5'N, 70°36.9'W, 570 m, 9 May 1995, Mathis, 2♂, 1♀ (NMNH); same, but 16 May 1998, 1♂ (NMNH). Salto Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 9 May 1995, Flint, 5♂ (NMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 1♂ (FSCA). **Monseñor Nouel Province** [not La Vega as labelled]: 6 km [not mi as labelled] NW Rt.1 on road to Constanza, 27 June 1998, Woodruff & Baranowski, 2♂, 1♀ (FSCA). 6.3 km W Bonao [jct. Carretera Duarte and rt. 12], 19°01.6'N, 70°28.9'W, 670 m, 29 March 1999, Mathis, 1♂ (NMNH). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 2♂ (NMNH). **Peravia Province:** 10 km E San José de Ocoa, 18°35'N, 70°25.6'W, 21 May 1998, Mathis, 6♂, 2♀ (NMNH).

Metrichia kumanskii (Botosaneanu)
(Fig. 21)

Ochrotrichia (*Metrichia*) *kumanskii* (Botosaneanu), 1991a:128 [♂, ♀, Haiti].

Metrichia kumanskii (Botosaneanu): Flint, Holzenthal, & Harris, 1999:100 [to *Metrichia*].

The species was described from Haiti and is here recorded from the Provinces of La Vega and Monseñor Nouel in the Dominican Republic. The genitalia of the example from Monseñor Nouel appears to be exactly as figured for the type, but the inferior appendage of the example from La Vega differs slightly. The apical point which is strongly attenuate in the type is here much shortened; there appears to be no other genitalic or abdominal difference between the two specimens.

A subspecies, *M. kumanskii jamaicae* has been described from Jamaica. It was held to differ from the typical form primarily in possessing the comma-shaped pouches between segments 6 and 7. Our two examples from the Dominican Republic both possess these marks as well as the pair of small sacs between segments 4 and 5, thus calling into question the distinctness of the Jamaican form.

Material Examined.—DOMINICAN REPUBLIC. **La Vega Province:** La Ciénega de Manabao, Park Headquarters, 3000 ft. [ca. 915 m], 3–5 July 1999, R.E. Woodruff, 1♂ (FSCA). **Monseñor Nouel Province** [not La Vega as labelled]: 6 km [not mi as labelled] NW Rt.1 on road to Constanza, 27 June 1998, Woodruff & Baranowski, 1♂ (FSCA).

Metrichia longispiua Flint and Sykora, new species
(Fig. 22)

This is a species very similar to *M. cafetalera* and the following species in the general structure and form of the male genitalia, differing almost exclusively in the structure of the phallus. From both of these species it may be distinguished by the very long spine arising at midlength and lying beside the other phallic process which bears only a single, large, strongly curved spine.

The female differs from that ascribed to *M. cafetalera* in that the posterior margin of the venter of segment 7 is evenly rounded and its apodemes, which are attached to a small posteromesal plate, diverge at less than 90°.

Adult Male.—Length of forewing 2.5 mm. Color fuscous; head and thorax with silvery-white hair, forewings with irregular, longitudinal silvery markings. Abdomen with pair of small pockets between segments 6 and 7, each with comma-shaped dark structure within. Seventh sternum with very small ventromesal point. Genitalia: Eighth sternum less than twice as long as high; posterior margin slightly sinuate. Cercus small, ovoid. Tenth tergum membranous; lateral hook elongate, tip curved strongly ventrad. Inferior appendage as long as high in lateral aspect, posterior margin obtusely angulate, dorsal margin convex. Phallus conical basally, constricted before midlength and divided into two apical process, one

long, slender slightly sinuous, darkened, other, curved to opposite side, consisting of flat sclerite, convolute toward apex and bearing at midlength large, curved spine arising from large, dark, basal sclerite.

Female.—Seventh sternum with posterior margin evenly rounded. Seventh tergum on each side with strap-like sclerite, obliquely truncate and bearing row of 5–8 setae. Apodemes of seventh sternum attached to small internal sclerite near center of posterior margin, angle of divergence between apodemes slightly less than 90°.

Type Material.—Holotype, male: DOMINICAN REPUBLIC. [La Vega Province]: Convento, 12 km S. Constanza, 6–13 June 1969, Flint & Gómez (NMNH). Paratypes: 11.5 km S. of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, Flint, 1♂, 1♀ (NMNH). Nr. Aguas Blancas, 13.7 km SE Constanza, 18°51.6'N, 70°41.9'W, 1505 m, 7 May 1995, Flint, 1♀ (NMNH). La Ciénega de Manabao, National Park Headquarters, 3000 ft (ca. 900 m), 20–21 April 2000, Woodruff & Henry, blacklight trap, 1♀ (FSCA).

Metrichia squamigera Flint

Ochrotrichia (*Metrichia*) *squamigera* Flint, 1992:385 [♂, Puerto Rico].
Metrichia squamigera (Flint): Flint, Holzenthal, & Harris, 1999:101 [to *Metrichia*].

The species was described from a few examples taken over a small stream in the Luquillo Mountains of eastern Puerto Rico. The male from the Dominican Republic has been compared with the holotype and found to be identical. A female from each country also has been compared and found identical, providing additional confirmation of the specific identity and the correct association of sexes.

Material Examined.—DOMINICAN REPUBLIC. **Independencia Province:** La Descubierta, 0 m, 18°34.1'N, 71°43.8'W, 25 March 1999, Flint, 1♂, 1♀ (NMNH).

Metrichia sp.

These females from Haiti have been compared with the allotype of *M. kumanskii*. They are very nearly alike, but there are enough small differences that we are unwilling to consider this a firm identification.

Material Examined.—HAITI. **Département de L'Ouest:** Parc National La Visite, Pic La Visite, 2100 m, 11 May 1984, blacklight, Thomas, 2♀ (FSCA).

Genus *Neotrichia* Morton

This genus, as well as the entire tribe Neotrichiini, is limited to the New World, primarily the Neotropical realm. Although a number of species are known from the United States and Canada, the greatest number, around 85, are found in Central and South America and the West Indies.

Larvae were first described by Ross (1944) and subsequently by various authors (Botosaneanu, 1994b; Flint, 1964; Wiggins, 1996). The larvae construct small,

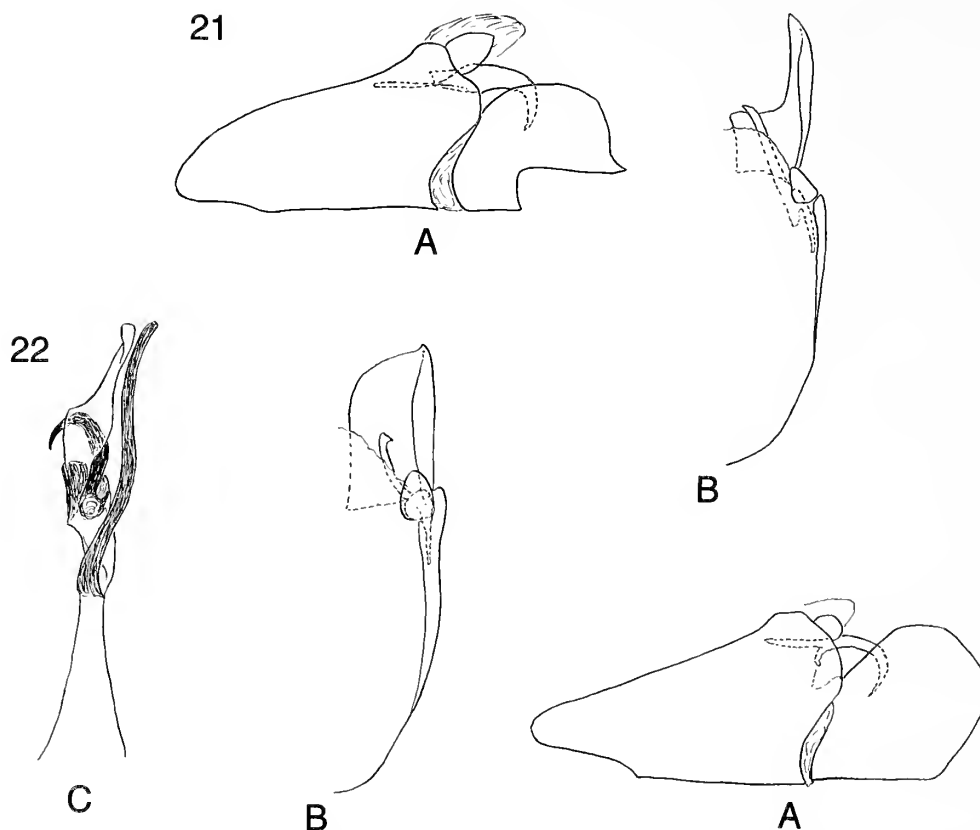


Fig. 21.—*Metrichia kumanski* (Botosaneanu), male genitalia: A. Lateral. B. Ninth and tenth terga and inferior appendage, dorsal.

Fig. 22.—*Metrichia longispina* new species, male genitalia: A. Lateral. B. Ninth and tenth terga and inferior appendage, dorsal. C. Phallus, dorsal.

tapered cases of small sand grains and are found in streams and rivers on and under rocks and boulders. Adults are commonly taken in large numbers at light near the larval habitat.

Neotrichia iridescens Flint

Neotrichia iridescens Flint, 1964:51 [♂, ♀, larva, case]. Flint, 1968a:37 [Jamaica, ♂, ♀, larva, case]; Flint, 1968b:48 [Dominica, St. Lucia, ♂, ♀, larva, case]; Botosaneanu, 1979:51 [Cuba]; Botosaneanu, 1989:99 [Martinique]; Botosaneanu, 1991a:128 [Haiti]; Botosaneanu, 1994a:43 [Guadeloupe]; Botosaneanu, 1995:32 [Dominican Republic]; Botosaneanu and Hyslop, 1998:18 [Jamaica].

This species is widely distributed over the Greater and Lesser Antilles: Cuba, Jamaica, Hispaniola, Puerto Rico, Guadeloupe, Dominica, St. Lucia, and Martinique. It has not yet been taken on any of the more southern Lesser Antillean Islands: St. Vincent, Grenada, Tobago, or Trinidad. It has been recorded from the provinces of Independencia and Pedernales in the Dominican Republic, and here from the additional provinces of Azua, El Seibo, La Altagracia, Monseñor Nouel, and Puerto Plata.

Material Examined.—DOMINICAN REPUBLIC. **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 1♂, 1♀ (CMNH). **El Seibo Province:**

Río Quisibani, E El Seibo, 18°45.3'N, 68°55.7'W, 12 May 1995, Flint, 3♀ (NMNH). Pedro Sanchez, small stream, 10 June 1976, Woodruff, 29♂, 59♀ (FSCA). **Independencia Province:** Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 1♂ (NMNH). Río Guyabal, 4.5 km N Postrer Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 1♂, 3♀ (NMNH). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 28♂, 31♀ (FSCA, NMNH, CMNH). **Monseñor Nouel Province:** Hotel Jacaranda, Bonao, 27–28 June 1998, Woodruff & Baranowski, 1♂, 1♀ (FSCA); same, but 18 April 2000, Woodruff & Henry, 1♂, 2♀ (FSCA). **Pedernales Province:** N Cabo Rojo, km 24, 3000 ft (915 m), 2 July 1998, Woodruff & Baranowski, 1♀ (FSCA). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 2♂, 8♀ (NMNH).

Neotrichia bifurcata Harris, new species (Fig. 23)

The genitalic appearance of *N. bifurcata* resembles that of *N. gotera* Flint from Argentina. Both species have the ventral process from the subgenital plate, a feature also seen in *N. bullata* Flint, both have spine-like processes from segment X, although this character is much more developed in the new species, and both have phallic apices forked. The new species is easily recognized by the elongate, bifid inferior appendages, and the structure of both the subgenital plate and segment X.

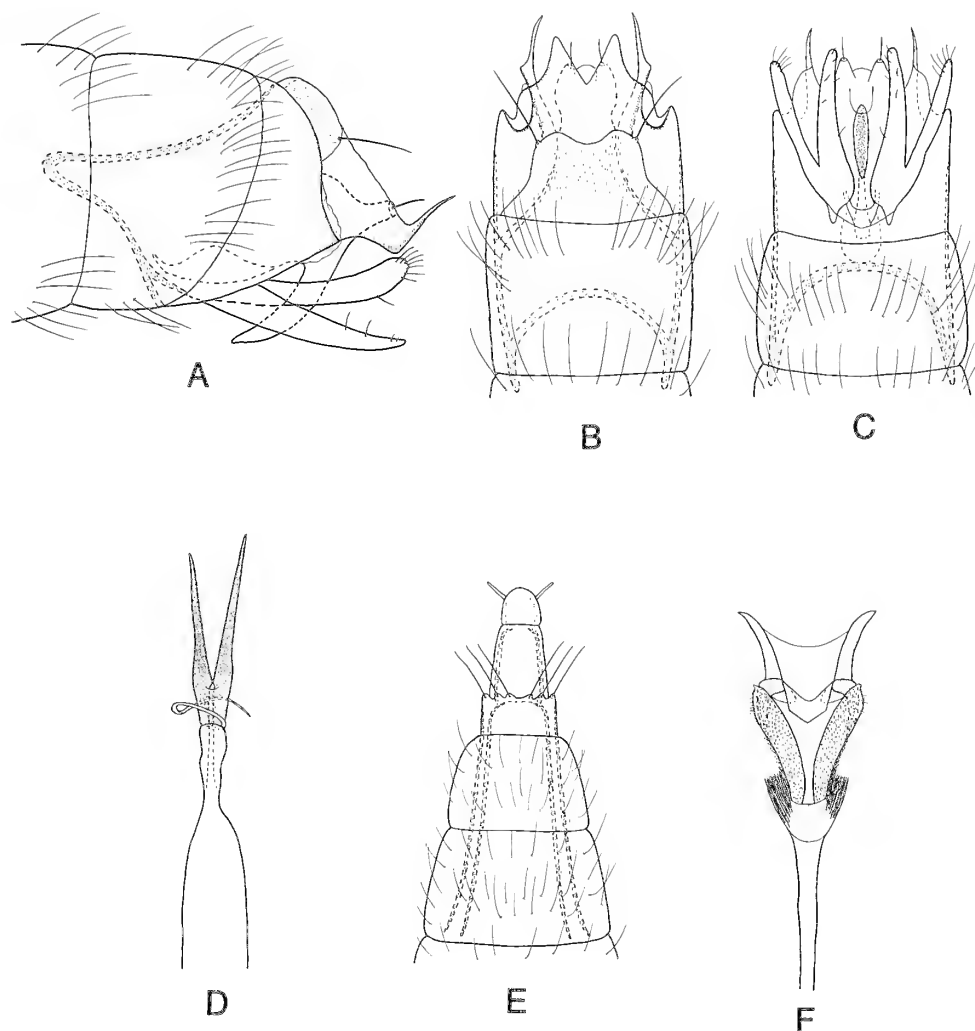


Fig. 23.—*Neotrichia bifurcata* Harris, new species, male genitalia: A, Lateral. B, Dorsal. C, Ventral. D, Phallus, dorsal. Female genitalia: E, Ventral. F, Vaginal sclerites, ventral.

Adult Male.—Length of forewing, 1.7 mm. Color brown in alcohol. Antenna with 18 segments. Abdominal segments VII and VIII annular. Genitalia: Segment IX with anterolateral margin bearing short, narrow lobe extending into segment VII; in dorsal view narrow, deeply emarginate anteriorly, posteriorly with lateral margins divided into thin apodemes. Tergum X complex, in lateral view with dorsum lobate bearing elongate seta from posterior margin, venter tapering downward to elongate, upturned acuminate process; in dorsal view lobate anteriorly, posteriorly deeply incised, lateral acuminate process protruding apically. Inferior appendage bifid in lateral view, upper portion thin and rounded apically, lower portion thin and gradually tapering distally; in ventral view split to near base, outer portion thin and rounded anteriorly, inner portion thin slightly tapering apically and slightly curved along mesal margin. Subgenital plate in lateral aspect with elongate ventral

process curving and tapering distally, posterior process narrowing apically and bearing stout seta; in ventral view divided into pair of seta-bearing lobes apically, ventral process appearing as oblong, sclerous plate. Phallus forked distally and heavily sclerotized, ejaculatory duct thin and short, emerging at base of fork, spiral process encircling shaft at midlength.

Female.—Length of forewing, 1.8 mm. Color brown in alcohol. Antenna with 18 segments. Abdominal segments VI and VII annular. Genitalia: Abdominal segment VIII with ring of setiferous lobes on posterior margin; internally with lateral apodemes arising from lateral margins and extending through segment VI. Segment IX rectangular with internal, lateral sclerites giving rise to anterolateral apodemes extending through segment VI. Segment X short, rounded apically, bearing pair of lateral papillae. Vaginal sclerites complex, consisting of several sclerotized plates, antermost plate small, fringed with

profuse hairs, and giving rise to pair of narrow, lateral plates extending posteriad and gently curving outward, lateral margins covered with short hairs, ventral surface with short protuberances, posteromesally with chevron-shaped plate, posterolaterally with pair of thin, club-shaped plates curving inward and giving rise to roughly rectangular structure with sclerous lateral margins.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. Pedernales Province:** Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, J. Rawlins, C. Young, S. Thompson, J. Davidson (CMNH). Paratypes: Same data, 2♂, 1♀ (CMNH, NMNH).

Neotrichia pequenita Botosaneanu

Neotrichia pequenita Botosaneanu, 1977:277 [Cuba, ♂]. Botosaneanu, 1990:46 [Barbados, ♂, ♀]; Botosaneanu, 1991a:128 [Haiti]; Botosaneanu, 1994b:458 [Cuba, larva]; Botosaneanu and Alkins-Koo, 1993:18 [Trinidad]; Botosaneanu and Hyslop, 1998:18 [Jamaica].

Neotrichia species 1 Kumanski, 1987:23 [♀]. **New synonym.**

The recorded distribution of this species is scattered over the Greater and Lesser antilles: Cuba, Jamaica, Haiti, Barbados, and Trinidad. Although known from several localities in Haiti, it had not been recorded from the Dominican Republic before. We have a few examples from the provinces of Independencia, La Altagracia, Monseñor Nouel, and Monte Cristi.

Comparison of the figures of females in Botosaneanu (1990, Fig. 26), Kumanski (1987, Fig. 15a) and our material leave little doubt but that all refer to the same species, association based on the Barbadian collections of Botosaneanu.

Material Examined.—**DOMINICAN REPUBLIC. Independencia Province:** Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 1♀ (NMNH). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 1♂ (FSCA). **Monseñor Nouel Province:** Río Yuna, Bonao, 600 ft [ca. 180 m], 18 April 2000, Woodruff & Henry, 1♂ (NMNH). **Monte Cristi Province:** Monte Cristi, 4 June 1986, Miller & Stange, 1♀ (FSCA).

Neotrichia species

Neotrichia sp. Botosaneanu, 1991a:130.

Botosaneanu records a single female in poor state from the southern arm of Haiti. It is stated not to be either *N. iridescens* or *N. pequenita*. However, with the discovery of *N. bifurcata* in southwestern Dominican Republic it is quite possible that Botosaneanu's specimen is the female of *N. bifurcata*. It is, therefore, not counted as an additional insular species.

Genus *Ochrotrichia* Mosely

This genus, together with the two preceding genera, is exclusively New World in distribution. It is well represented throughout, with nearly 90 species, and four fossil species, described to date (Wichard, 1981; Wells and Wichard, 1989). All the Greater Antillean islands hold at least four species, with Hispaniola bearing a minimum of eight.

Ross (1944) first described the larvae of this genus, and other species have been described since (Wiggins, 1996). The larvae make cases of silk, sand, and/or algal pieces, often with a pair of short, tubular, dorsal projections (Botosaneanu and Flint, 1982). Most are compressed, purse-like in form, but some are depressed with the ventral valve flat against the substrate. Most inhabit flowing waters of many types, but some, especially those with flattened cases, are inhabitants of the madicolous habitat. Some feed by scraping diatoms from the substrate.

Ochrotrichia baorucoensis Flint and Sykora, **new species** (Fig. 24)

This and the Jamaican *O. caligula* Flint are clearly sister species, based on the overall structure of the male genitalia. *Ochrotrichia baorucoensis* is to be distinguished by the apex of the tenth tergum which is pointed on both sides, the inferior appendage bears a small lobe with several black setae ventromesally, and the darkened apical process of the phallus is scythe-shaped rather than curled around the pale process.

The Larimar mine locality produced males and females of three species, the sexes of only *O. larimar* n. sp. seem to be clearly associated. The males and females of this and *O. verda*, also taken in the same collection, cannot be unequivocally associated.

Adult Male.—Length of forewing, 3 mm. Color gray, mostly denuded; antennae, legs and venter stramineous; head, thorax dorsally, and forewing gray, latter with indication of pale transverse line at midlength. Seventh sternum with elongate, anteromesal process. Genitalia: Ninth segment tubular, tergum neither depressed nor produced anteriorly, with large, rounded lobe from posterodorsal margin. Tenth tergum elongate, heavily sclerotized laterally, apex with mesal, U-shaped excision, apicolaterally produced into sharp point. Inferior appendage rather boot-shaped in lateral aspect, ventral margin with small, mesal lobe; apex with band of short, dark, peglike setae, mesal lobe with 3–4 such setae. Phallus barely longer than genital capsule, divided at nearly midlength into two apical processes, one darkened, scythe-shaped, other pale, tubular.

Female.—Not certainly associated.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. Barahona Province:** San Rafael, 8.3 km S of Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 15 May 1995, O.S. Flint, Jr. (NMNH). Paratypes: Larimar Mine, nr. Filipinas, 26 June–7 July 1992, Woodruff & Skelley, 2♂ (FSCA, NMNH).

Ochrotrichia cachonera Botosaneanu

Ochrotrichia cachonera Botosaneanu, 1995:23 [♂, ♀].

The holotype was described from Independencia Province, and we here record males from three more localities in the provinces of Barahona, La Vega, and

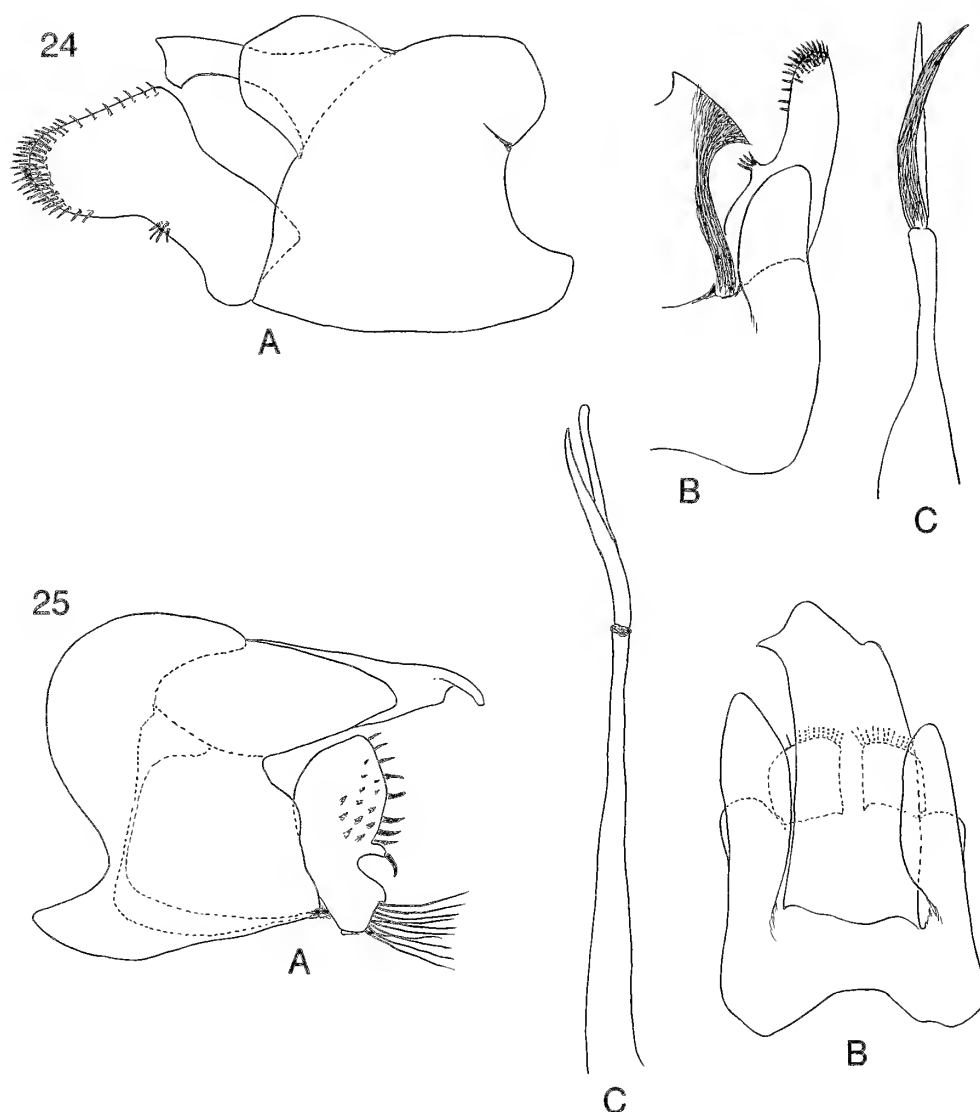


Fig. 24.—*Ochrotrichia baorucoensis* new species, male genitalia: A, Lateral. B, Dorsal. C, Phallus, dorsal.

Fig. 25.—*Ochrotrichia larimar* new species, male genitalia: A, Lateral. B, Dorsal. C, Phallus, dorsal.

Monseñor Nouel. The female allotype was from the Province of Monte Plata. The two females here recorded from Barahona and Hato Mayor Provinces, have been compared directly to the allotype and found identical. However, none of these females have been taken with associated males and thus there still is no proof that they are correctly associated.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** San Rafael, 8.3 km S of Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 15 May 1995, Flint, 8♂ (NMNH, CMNH). **Larimar Mine, nr. Filipinas,** 26 June–7 July 1992, Woodruff & Skelley, 1♀ (FSCA). **Hato Mayor Province:** Mango Limpio, 23 km N Hato Mayor, 9 June 1986, Woodruff & Stange, 1♀ (FSCA). **La Vega Province:** Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 1♂ (NMNH). **Monseñor Nouel Province** [not La Vega as labelled]: 6

km [not mi as labelled] NW Rt.1 on road to Constanza, 27 June 1998, Woodruff & Baranowski, 1♂ (FSCA). [**Monte Plata Province:** Arroyo Los Verros, Sierra de Agua, 29 April 1995, Botosaneanu, 1♀ allotype (ZMUA).

Ochrotrichia ingloria Botosaneanu

Ochrotrichia ingloria Botosaneanu, 1995:25 [♂, ♀].

The types of this species were taken in the same localities as the previous species in the provinces of Independencia and Monte Plata. We have one more series from Pedernales Province.

Material Examined.—DOMINICAN REPUBLIC. **Pedernales Province:** Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 8♂ (CMNH, NMNH).

Ochrotrichia larimar Flint and Sykora, **new species**
(Fig. 25)

This species is a very close relative to *O. spinosissima* Flint which is known from Puerto Rico and Dominica. From the typical *O. spinosissima* specimens, *O. larimar* differs by the tenth tergum extending proportionately further beyond the dorsolateral lobes of the ninth segment and its tip being more strongly asymmetrical and bearing a point to its right side, the inferior appendage is proportionately much higher than long, and the apical appendages of the phallus are only half the length of the basal portion (the apical section is only as long as the basal section in *O. spinosissima*).

The females of this species seem to be firmly associated, based on a large collection containing both sexes and the similarity of their terminalia to those of the closely related *O. spinosissima* from Puerto Rico and Dominica. It is now apparent that the female described by Flint (1964) as that of *O. marica* (Fig. 16 N) is that of *O. spinosissima* (c.f. Flint, 1968b, Fig. 162). The Hispaniolan females have a similar elongate plate apicoventrally from the eighth sternum but it is proportionately more slender and only barely expanded apicad.

Adult Male.—Length of forewing, 2.5 mm. Color brown in alcohol; probably identical to that of female. Seventh sternum with elongate, mesal process. Genitalia: Ninth segment tubular, tergum neither depressed nor produced anteriad, with large, rounded lobe from posterodorsal margin. Tenth tergum elongate, slightly curved plate, apex asymmetrical with lateral point to right side. Inferior appendage higher than long in lateral aspect, posteroventral lobe bearing brush of long setae, posterodorsal margin with row of stout black setae, ventralmost seta borne from elongate base, mesal face with several more black, pointed setae. Phallus divided at apical third into two apical processes one darkened, slightly curved and acute apically, other pale, tubular.

Female.—Length of forewing, 2.5–3 mm. Color fuscous; antennae, legs basally and venter stramineous; head and thorax laterally with white hair; tarsi of mid- and hindlegs annulate; forewing fuscous with white transverse line at midlength and small white spots along margin. Genitalia: Eighth sternum with elongate apicomesal lobe, slightly more than twice as long as wide, slightly broadened apically. Spermathecal sclerite as in Flint, 1968b, Fig. 163.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. Barahona Province:** Larimar Mine, nr. Filipinas, 26 June–7 July 1992, Woodruff & Skelley (FSCA). Paratypes: Same data, 4♂, 7♀ (FSCA, NMNH, CMNH). [**La Vega Province:** 20 km S Constanza, 3–7 June 1969, Flint & Gómez, 1♀ (NMNH). [**La Vega Province:** La Palma, 12 km E El Río, 2–12 June 1969, Flint & Gómez, 1♀ (NMNH).

Ochrotrichia obovata Flint and Sykora, **new species**
(Fig. 26)

Based on the structure of the phallus, and the ninth and tenth segments, this species apparently is related to

O. caramba Botosaneanu (Cuba), *O. cachonera* Botosaneanu (Dominican Republic), *O. spinosissima* Flint (Puerto Rico, Dominica), and *O. villarenia* Botosaneanu (Cuba). From all these it is immediately distinguished by having an elongate, apically-rounded, inferior appendage with many, short, peglike setae along its ventral margin.

Adult Male.—Length of forewing, 3.5 mm. Color in alcohol: uniformly pale brown. Seventh sternum with distinct, short, apicomesal point. Genitalia: Ninth segment tubular, tergum neither depressed nor produced anteriad, with large, rounded lobe from posterodorsal margin. Tenth tergum elongate, parallel-sided lobe shallowly divided apicomesally. Inferior appendage almost four times as long as broad, apex rounded, dorsal and ventral margins subparallel; with band of black, peglike setae around apex and along ventral margin. Phallus almost twice as long as genital capsule, divided at nearly midlength into two apical processes one darkened, other pale.

Female.—Unassociated.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC. [La Vega Province:]** 20 km S Constanza, 3–7 June 1969, Flint & Gómez (NMNH).

Ochrotrichia seiba Flint and Sykora, **new species**
(Fig. 27)

This species is very closely related to the Jamaican *O. insularis* Mosely and the Cuban *O. ayaya* Botosaneanu, and is the unquestioned representative of this group found on Hispaniola. This species agrees most closely with *O. ayaya* in the shape of the tenth tergum, although both lobes are more nearly equal in size and the apices are not upturned, but agrees more with *O. insularis* in the shape of the inferior appendage which lacks a ventromesal extension. The apical point of the ventromesal spine with U-shaped base is much longer and directed posteriad in *O. seiba*, rather than being barely longer than broad and angled laterad as it is in both the other species. The basodorsal spine arises from its lobe at a shallow, acute angle rather than being strongly arched basally.

All the available males have been checked to determine if they, too, have the basodorsal spine of the tenth tergum borne in two, mirror-image versions as has been shown for *O. insularis* (Botosaneanu and Hyslop, 1998). All the 16 males are identical, and of the “sinistral” morph, as shown. This is another difference from *O. insularis* in which 24 examples were found to be “dextral” and 13 “sinistral.”

The females of this species and *O. cachonera* are very similar and have been compared side-by-side. There are enough differences, mostly small, so that we believe them to represent two truly distinct species. The greatest difference is in the internal apodemes which only reach slightly beyond the anterior border of the seventh sternum in *O. cachonera*, but into the fifth segment in *O. seiba*.

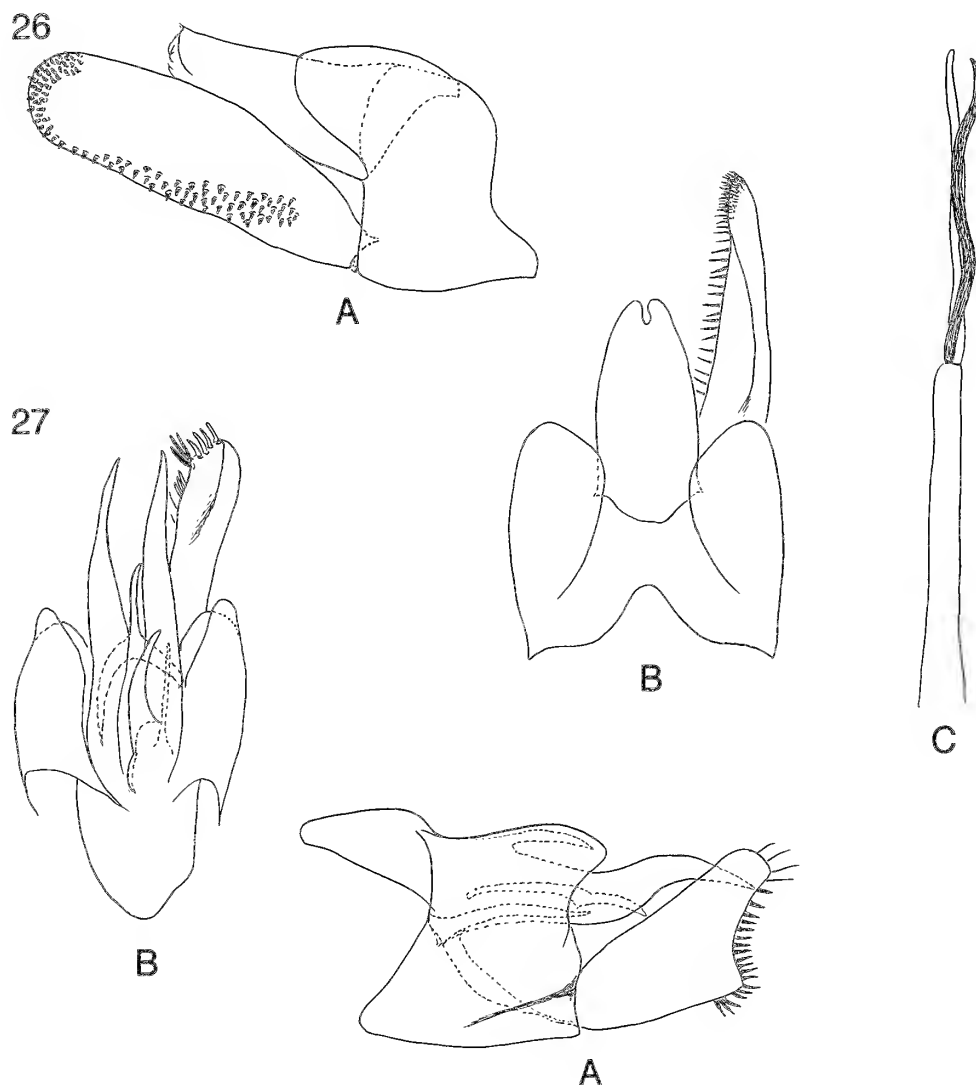


Fig. 26.—*Ochrotrichia obovata* new species, male genitalia: A, Lateral. B, Dorsal. C, Phallus, dorsal.

Fig. 27.—*Ochrotrichia seiba* new species, male genitalia: A, Lateral. B, Dorsal.

Adult Male.—Length of forewing, 2.5–3 mm. Color in alcohol: uniformly pale brown. Seventh sternum with minute, apicomesal point. Genitalia: Ninth segment tubular, tergum depressed and produced anteriorly, with large, rounded lobe from posterodorsal margin. Tenth tergum consisting of two elongate lobes, tapering to apical points roughly equal in shape; base of left process with basodorsal spine arising from lobe at acute angle; slender spine ventrally on left side and ventral U-shaped sclerite bearing elongate, slender spine apicomesally. Inferior appendage barely longer than high in lateral aspect with distinct posteroventral angle; posterior margin with row of short, black spines and small cluster of such spines barely separated from this row on ventral margin. Phallus long, slender, without noticeable modifications.

Female.—Size and color as in male. Genitalia: Eighth sternum with small, posteroventral, rounded lobe; apodemes attached laterally near posterior margin, extending anteriorly into fifth segment. Spermathecal sclerite with long anterior lobe and posterior arms (c.f. Flint, 1968a, fig. 125).

Type Material.—Holotype, male: **DOMINICAN REPUBLIC, El Seibo Province:** Pedro Sanchez, small stream, 10 June 1976, R.E. Woodruff (FSCA). Paratypes: Same data, 14♂, 34♀ (FSCA, NMNH, CMNH). **Elias Peña Province:** Rio Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 1♂ (FSCA).

Ochrotrichia serra Botosaneanu

Ochrotrichia (*O.*) *serra* Botosaneanu, 1991a:125 [Haiti, ♂].

The species was described from one locality in Haiti. We have no new material.

Ochrotrichia verda Flint

Ochrotrichia (*O.*) *verda* Flint, 1968c:153 [Puerto Rico, ♂].

The unique holotype of this species is from the mountains of eastern Puerto Rico. It has been compared side-by-side with the specimen from the Larimar Mine in southwestern Dominican Republic and been found to be identical.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** Larimar Mine, nr. Filipinas, 26 June–7 July 1992, Woodruff & Skelley, 1♂ (FSCA).

Ochrotrichia species A

The Larimar mine locality produced males of three species and females of four species, the sexes of only *O. larimar* seem to be clearly associated. A second female species agrees with females tentatively associated with *O. cachonera*. The males of *O. baorucoensis* and *O. verda* cannot be unequivocally associated with either of the remaining two female forms, although it is tentatively suggested that species A might be the female of *O. baorucoensis*.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** Larimar Mine, nr. Filipinas, 26 June–7 July 1992, Woodruff & Skelley, 3♀ (FSCA).

Ochrotrichia species B

These females might be associated with *O. verda*, *O. baorucoensis* (males of both being taken at the same site), or some other species otherwise unknown at the site.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** Larimar Mine, nr. Filipinas, 26 June–7 July 1992, Woodruff & Skelley, 2♀ (FSCA).

Genus *Orthotrichia* Eaton

A genus of around 75 species with a wide distribution throughout the world, it seems most speciose and diverse in southeast Asia, Australia, and Africa. There are six species described from North America, two of which have ranges extending into Central America and/or the Greater Antilles. One new species has recently been described from the Amazon basin in Peru.

The larvae are well known, constructing silken cases (Nielsen, 1948; Wells, 1985; Wiggins, 1996). They are usually associated with aquatic vegetation and filamentous algae in standing waters, but Wells (1985) recorded them from rocks in flowing waters with no obvious filamentous algae.

Orthotrichia aegerfasciella (Chambers)

Clymene aegerfasciella Chambers, 1873:114.

Orthotrichia americana Banks, 1904:116. Ross, 1944:140 [♂, ♀, distribution]; Flint, 1966:135 [to synonymy]; Botosaneanu, 1979:49 [Cuba].

Orthotrichia aegerfasciella (Chambers): Botosaneanu, 1991a:132 [Haiti].

The species has a wide distribution in eastern North America, being known from Canada south to Florida and west to Texas. It has been recorded from Cuba and Haiti in the Antilles, and Panama on the mainland. We here record it for the first time from the Dominican Republic, with records from the provinces of Barahona, La Altagracia, and La Romana.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** 24 km E Barahona, 27 September 1985, Woodruff & Stange, 1♀ (FSCA). 5 km NW Barahona, Agricultural Experiment Station, 29–30 April 1978, Woodruff et al., 2♀ (FSCA). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, blacklight, 41♂, 13♀ (FSCA, NMNH, CMNH); same, but sweeping, 1♂ (FSCA). Higueral, 19 March 1985, Woodruff & Drummond, 6♂, 1♀ (FSCA). **La Romana Province:** La Romana, 16 September 1976, Folch, 1♀ (FSCA).

Orthotrichia cristata Morton

Orthotrichia cristata Morton, 1905:75. Ross, 1944:141 [♂, ♀, distribution]; Flint, 1968a:45 [♂, ♀, Jamaica]; Botosaneanu, 1979:49 [Cuba].

This species has a distribution rather like that of the preceding species: Canada south to Florida, west to British Colombia and Texas, plus Cuba and Jamaica in the Greater Antilles. These are the first records for Hispaniola. It was taken in the provinces of Barahona, La Altagracia, and La Romana, at both ends of the Dominican Republic.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** 5 km NW Barahona, Agricultural Experiment Station, 29–30 April 1978, Woodruff et al., 2♀ (FSCA). **La Altagracia Province:** Higueral, 19 March 1985, Woodruff & Drummond, 5♂, 19♀ (FSCA, NMNH, CMNH). **La Romana Province:** La Romana, 16 September 1976, Folch, 5♂, 13♀ (FSCA, NMNH).

Genus *Oxyethira* Eaton

Oxyethira is a very large genus of Hydroptilini, with several hundred species known world-wide, over 75 species having been described from the Neotropics alone. They are found in all parts of the New World from Chile to the Arctic including both the Greater and Lesser Antilles. Kelley (1984) reviewed the genus and placed its species in several subgenera.

Larvae are well known and build distinctive flask-shaped cases of silk (Nielsen, 1948; Wiggins, 1996). Larvae are said to inhabit slow-moving or standing waters in vegetation or filamentous green algae, but are also frequently found on rocks in flowing waters (Wells, 1985). They are recorded as feeding on filamentous algae by puncturing the cells and feeding on the contents, but diatoms and entire algal filaments also have been found in the gut (Wiggins, 1996).

Oxyethira (Mesotrichia) albaeaequae Botosaneanu

Oxyethira (Dampftrichia) [sic] albaeaequae Botosaneanu, 1995:30 [♂, ♀, Dominican Republic].

This recently described species has only been taken in the province of La Vega in the Cordillera Central at 1000 m. and above. The material here recorded is all from the same area.

We are transferring the species to the subgenus *Mesotrichia*: see comments under *O. geminata* new species.

Material Examined.—DOMINICAN REPUBLIC. **La Vega Province:** El Convento, 12 km SE Constanza, 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 21♀ (NMNH). 11.5 km S of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, Flint, 4♀ (NMNH). Near Alto Bandera Pass, Res. Sta. Fund. Moscoso Puello, 2400 m, 8–9 May 2001, Woodruff & class, 18♂, 9♀ (FSCA, NMNH). Cordillera Central, Convento, waterfall "Agua Blanca," 11 May 1995, L. Botosaneanu, light, 1♂, 2♀ topotypic paratypes (ZMUA).

Oxyethira (Dampftrichia) mirebalina Botosaneanu

Oxyethira (Dampftrichia) mirebalina Botosaneanu, 1991a:130 [♂, ♀, Haiti]. Botosaneanu, 1995:29 [Dominican Republic].

Originally described from Haiti, it has since been recorded from the provinces of Duarte, La Vega, and Monte Plata. Our record is also from the province of La Vega.

Material Examined.—DOMINICAN REPUBLIC. **La Vega Province:** Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 19–21 May 1995, Flint, 12♂, 1♀ (NMNH).

HAITI. [Département de l'Ouest]: Grande rivière de l'Artibonite à Mirebalais, 27 Nov 1979, Botosaneanu, light, 1♂ holotype (ZMUA).

Oxyethira (Mesotrichia) geminata
Flint and Sykora, new species
(Fig. 28)

The species appears to belong to the subgenus *Mesotrichia*, agreeing with the basic characteristics outlined by Kelley (1984) for this subgenus. In addition to *O. geminata* and *O. scopulina* n. sp., it seems apparent that *O. longispinosa* Kumanski (Cuba), *O. ortizorum* Botosaneanu (Dominican Republic), and *O. albaeaequae* Botosaneanu (Dominican Republic) all should be placed in *Mesotrichia* together with the type species *O. jamaicensis* Flint (Jamaica). The subgenus thus contains six species, all from the Greater Antillean islands. *Oxyethira geminata* is most similar to *O. jamaicensis* and *O. albaeaequae* as all three species lack an elongate posterolateral lobe from the eighth segment. From these it is distinguished by the form of the subgenital processes which has, in ventral aspect a single mesal point; in *O. jamaicensis* there are two points, and in *O. albaeaequae* it is bandlike with no points. The phallus in *O. geminata* ends in two separate processes, each tipped with a dark spine, in *O. albaeaequae* there is only one spine. *Oxyethira jamaicensis* has two, dark, apical spines, but they arise from a single lobe. The females of *O. geminata* and *O. jamaicensis* both have a bilobed

eighth sternum, but *O. jamaicensis* has well-developed, cuplike, basolateral pockets which are lacking on *O. geminata*. The apex of the eighth sternum in *O. albaeaequae* is developed into a single, mesal projection.

Adult Male.—Length of forewing, 2.5–3 mm. Color pale brown, forewing with two black spots, one in center, other on posterior margin before midlength, fringe mostly fuscous. Seventh sternum with large, apicomesal, pointed process. Genitalia: Eighth segment deeply divided ventromesally, posterolateral margin rounded. Ninth segment greatly produced anteroventrally into sixth segment; dorsal margin near posterior bearing elongate, pointed process (varying in width and curvature between specimens). Tenth tergum membranous. Subgenital plate band-like, decurved apically, bearing darkened, mesal point in ventral aspect. Bilobed process with apicolateral angles slightly developed in ventral aspect, bearing terminal seta. Inferior appendage short, blackened point in lateral aspect; black, partially fused mesally and produced posterolaterally in ventral aspect (varying in degree of fusion and length between specimens). Phallus long, slender, tubular basally, narrowing apically into slender, strap-like sclerite; apically with pair of elongate, arched spines (varying in length and degree of twisting between specimens) one arising from end of strap-like sclerite, other with more membranous attachment; ejaculatory duct internally, continuing through strap-like sclerite.

Female.—Size and color as in male. Genitalia: Sixth sternum with distinct apicomesal point. Eighth sternum produced into darkened, rectangular, posterior projection, partially divided mesally in ventral view; produced anterolaterally into large, darkened lobes, truncate anteriorly and widely separated mesally in ventral view. Eighth tergum appearing to lack anterolateral apodemes, produced dorsad in lateral view. Spermathecal sclerite almost wholly membranous, elongate and complex with anterior ring-like sclerite.

Type Material.—Holotype, male: DOMINICAN REPUBLIC. **La Vega Province:** 11.5 km S of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, W.N. Mathis (NMNH). Paratypes: Same, but Flint, 1♂, 3♀ (NMNH). **Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°40'N, 70°36'W, 1850 m, 5–6 August 1990, Rawlins & Thompson, 3♂, 7♀ alcohol (CMNH).

HAITI. Département de l'Ouest: Parc National La Visite, Pic La Visite, 2100 m, 11 May 1984, blacklight, Thomas, 1♂, 12♀ (FSCA); same, but basecamp, 1980 m, 19 May 1984, 3♀ (FSCA).

Oxyethira (Mesotrichia) ortizorum Botosaneanu

Oxyethira (Dampftrichia) [sic] ortizorum Botosaneanu, 1995:29 [♂, Dominican Republic].

The males of this uncommon species are rarely collected, although the females are not infrequently taken at high elevations. The holotype has been compared directly to a cleared male from "the Larimar Mine" and found to agree very closely. The only difference noted is in the darkened, oval plate on sternum nine: in the

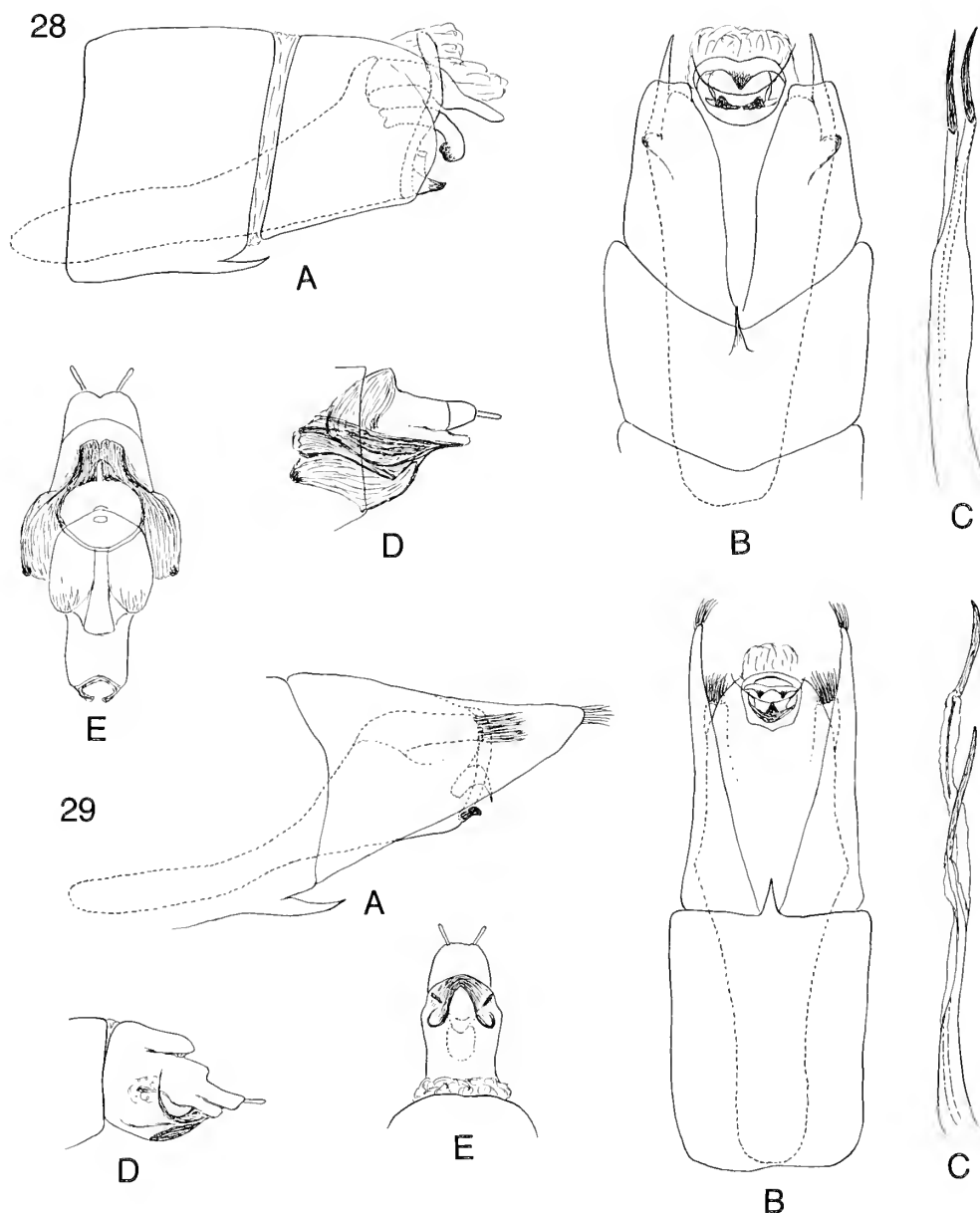


Fig. 28.—*Oxyethira geminata* new species, male genitalia: A, Lateral. B, Ventral. C, Phallus, dorsal. Female genitalia: D, Lateral. E, Ventral.

Fig. 29.—*Oxyethira scopulina* new species, male genitalia: A, Lateral. B, Ventral. C, Phallus, dorsal. Female genitalia: D, Lateral. E, Ventral.

holotype, this is distinctly longer than wide, but in the "Larimar" material it is barely as long as wide. The two females associated with these three males are the basis for the assignment of a number of collections from the central mountains to this species. See the comments under *O. geminata* concerning the transfer of this species to the subgenus *Mesotrichia*.

In the addition to the collections from the Cordillera Central, La Vega Province at over 1000 m. elevation, it is here recorded from Barahona and Elias Piña Provinces at higher elevation sites.

Material Examined.—**DOMINICAN REPUBLIC.** **Barahona Province:** Larimar Mine, nr. Filipinas, 26 June–7 July 1992, Woodruff & Skelley, 3♂, 2♀ alcohol (FSCA, NMNH). **Elias Piña Province:** Río Limpio, 2400 ft. [ca. 730 m], 26–27 Apr 2000, Woodruff & Henry, blacklight trap, 3♀ (FSCA). [**La Vega Province:**] Cordillera Central, Jarabacoa, Los Dajaos, Arroyo El Dulce, 26 Apr 1995, Botosaneanu, light, 1♂ holotype (ZMUA). La Ciénega de Manabao, National Park Headquarters, 3000 ft [ca. 900 m], 3–5 Jul 1999, Woodruff, blacklight trap, 8♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 16♀ (FSCA, NMNH). 11.5 km S of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, Flint, 1♀ (NMNH).

Oxyethira (Mesotrichia) scopulina

Flint and Sykora, new species

(Fig. 29)

This species is closely related to *O. ortizorum* in that both have the posterolateral margin of the eighth segment produced into an elongate, apically rounded lobe and a long dorsolateral process from the ninth segment that ends in a large brush of setae. From *O. ortizorum*, *O. scopulina* may be distinguished by the dorsolateral process of the ninth segment being shorter than the posterolateral lobe of the eighth segment, in the structure of the subgenital plate and ninth sternal complex, and the possession of two elongate spines on the phallus. The female terminalia are distinguished by the looped dark mark laterally on the eighth segment and the indistinct internal sclerites.

Adult Male.—Length of forewing, 3–3.5 mm. Color pale brown, forewing with two black spots, one in center, other on posterior margin before midlength, fringe mostly fuscous. Seventh sternum with large, apicomesal, pointed process. Genitalia: Eighth segment deeply divided ventromesally, posterolateral margin produced into long plate, rounded apically. Ninth segment greatly produced anteroventrally through seventh segment; dorsal margin near posterior bearing elongate, broad process ending in brush of large setae, not attaining apex of eighth segment plate. Tenth tergum membranous. Subgenital plate band-like, bearing pair of sharp, ventrally directed points from apex. Bilobed process with apicolateral angles slightly developed in ventral aspect, bearing terminal seta. Inferior appendage short, blackened point in lateral aspect; small, black, mesal, triangular point in ventral aspect. Phallus long, slender, with short, tubular base, narrowing beyond into slender, strap-like sclerite with membranous side; with two long, slender, curved spines, one apically, other near midlength, both with membranous attachment; ejaculatory duct visible only in tubular base.

Female.—Size and color as in male. Genitalia: Sixth sternum with distinct apicomesal point. Eighth sternum produced into posteromesal lobe, bearing dark line directed anterolaterad, with lateral ends looped back posteriad, cuticle slightly darkened posteriad of this line. Eighth tergum appearing to lack anterolateral apodemes, slightly produced dorsad in lateral view. Spermathecal sclerite almost wholly membranous, and nebulous.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC.** **Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°40'N, 70°36'W, 1850 m, 5–6 August 1990, Rawlins & Thompson (CMNH). Paratypes: same data, 3♂, 4♀ (CMNH, NMNH). [**La Vega Province:** El Convento, 12 km SE Constanza, 18°51.5'N, 70°41.9'W, 1400 m, 6–13 June 1969, Flint & Gómez, 2♀ (NMNH).

Oxyethira (Dampftrichia) cirrifer Flint

Oxyethira cirrifer Flint, 1964:57 [♂, ♀, Puerto Rico]. Flint, 1968a:42 [♂, ♀, Jamaica]; Flint, 1968b:55 [Dominica]; Kelley & Morse, 1982:258 [to synonymy with *O. arizona* Ross]; Kumanski, 1987:26 [♀, Cuba]; Botosaneanu, 1989:101 [Martinique, as *O. arizona*]; Botosaneanu, 1991a:130 [Haiti]; Botosaneanu & Hyslop, 1998:16 [Jamaica, as valid species].

The exact status of *O. cirrifer* is not clear; Kelley and Morse (1982) believed it is a synonym of *O. arizona* Ross, but Botosaneanu and Hyslop (1998) thought it a valid species. All agree that the continental form is very close to the insular one. Under the name *O. cirrifer*, the species is reported from all the Greater Antillean islands and as far south in the Lessers as Martinique. On the mainland, *O. arizona* is known from the southwestern United States as far south as Costa Rica.

Although recorded from Haiti (Botosaneanu, 1991a), these are the first records from the Dominican Republic. We have seen it from the provinces of El Seibo, Hato Mayor, Independencia, La Altagracia, La Romana, Monte Cristi, and Pedernales, indicative of a wide distribution over the island.

Material Examined.—**DOMINICAN REPUBLIC.** **El Seibo Province:** Pedro Sanchez, small stream, 10 June 1976, Woodruff, 1♂, 1♀ (FSCA). **Hato Mayor Province:** Mango Limpio, 23 km N Hato Mayor, 9 June 1986, Woodruff & Stange, 2♂, 9♀ (FSCA, NMNH). **Independencia Province:** Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 2♀ (NMNH). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 2♀ (FSCA). Nisibón "Papagallo," 16–19 June 1998, Woodruff & Freytag, 1♂ (FSCA). Higueral, 19 March 1985, Woodruff & Drummond, 2♀ (FSCA). **La Romana Province:** La Romana, 16 September 1976, Folch, 2♀ (FSCA). **Monte Cristi Province:** Monte Cristi, 4 June 1986, Miller & Stange, 3♀ (FSCA). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 18 March 1999, Flint, 1♂, 2♀ (NMNH).

Oxyethira (Loxotrichia) janella Denning

Oxyethira janella Denning, 1948:397 [♂, USA]. Flint, 1968a:42 [♂, ♀, Jamaica]; Botosaneanu, 1991a:32 [Haiti]; Botosaneanu, 1995:32 [Dominican Republic]; Flint, 1996a:98 [Cuba, Hispaniola, Jamaica, Puerto Rico, Guadeloupe, and Dominica.]

Oxyethira neglecta Flint, 1964:57 [♂, ♀, Puerto Rico]. Flint, 1968a:42 [to synonymy].

This species is very close to *O. tica* Holzenthal and Harris, which was not recognized until 1992. As a consequence early records of *O. janella* from Barbados (Botosaneanu, 1990) and Martinique (Botosaneanu, 1989) need to be reconfirmed, as *O. tica* seems to be the only species known from south of Dominica.

In contrast to the Lesser Antilles, *O. janella* is the only species of the pair found on the Greater Antilles. It has been recorded from all the major islands and in Haiti and the Dominican Republic where it was known from Duarte, Independencia, La Vega, and Monte Plata Provinces. We here add the provinces of Azua, Barahona, Elías Piña, El Seibo, Hato Mayor, La Altagracia, La Romana, Monte Cristi, Pedernales, Puerto Plata, San Cristobal, and San Juan.

Material Examined.—**DOMINICAN REPUBLIC.** **Azua Province:** Sec. Canoa, Mirador de la Presa, Yaqui del Sur, 30 September 1978, Woodruff, 2♀ (FSCA). **Barahona Province:** San Rafael, 8.3 km S Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 22 March 1999, Flint, 13♂, 1♀ (NMNH). **Elías Piña Province:** Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 18♀ (FSCA). **El Seibo Province:** Río Quisibani, El Seibo, 18°45.3'N, 68°55.7'W, 12 May 1995, Flint, 3♂,

11♀ (NMNH). Pedro Sanchez, small stream, 10 June 1976, Woodruff, 20♂, 25♀ (FSCA). Hotel Santa Cruz, 28 May 1985, Woodruff & Stange, 2♀ (FSCA). **Hato Mayor Province:** Mango Limpio, 23 km N Hato Mayor, 9 June 1986, Woodruff & Stange, 1♂, 1♀ (FSCA). **Independencia Province:** La Descubierta, 3 August 1983, Woodruff, 3♂, 4♀ (FSCA). Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 2♂, 14♀ (NMNH). Río Guyabal, 4.5 km N Postre Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 3♂, 7♀ (NMNH). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 3♂, 6♀ (FSCA); same, but sweeping, 1♂ (FSCA). 2 km E Nisibón, Río Nisibón, 12 June 1986, Woodruff & Stange, 2♀ (FSCA). Higueral, 19 March 1985, Woodruff & Drummond, 6♂, 12♀ (FSCA). **La Romana Province:** La Romana, 16 September 1976, Folch, 2♂, 1♀ (FSCA). **La Vega Province:** Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 12♂, 38♀ (NMNH); same, but 19–21 May 1995, 10♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°09.9'N, 70°33.5'W, 980 m, 7 May 1995, Flint, 5♀ (NMNH). Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 2♀ (NMNH). El Convento, 12 km SE Constanza, 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 2♀ (NMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 6♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 4♀ (FSCA). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra", along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 1♀ (FSCA). **Monseñor Nouel Province:** Río Yuna, Bonao, 600 ft [ca. 180 m], 18 April 2000, Woodruff & Henry, 1♂, 6♀ (FSCA). **Monte Cristi Province:** Monte Cristi, 4 June 1986, Miller & Stange, 3♂, 25♀ (FSCA). **Monte Plata Province:** Bayaguana, 22 August–2 September 1991, Brown, 1♂, 2♀ (FSCA). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 18♂, 61♀ (NMNH); same, but 18 March 1999, 9♂, 12♀ (NMNH); same, but 20 March 1999, 13♂, 30♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 11♂, 7♀ (CMNH). 20.5 km N Cabo Rojo, 12 April 2000, Woodruff & Henry, 1♂, 3♀ (FSCA). N Cabo Rojo, km 21, 1200 ft. (365 m), 1 July 1998, Woodruff & Baranowski, 2♂, 1♀ (FSCA); same, but 19 June 1976, Woodruff, 1♂, 7♀ (FSCA). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 7♂, 146♀ (NMNH). **San Cristóbal Province:** La Trinidad, NE Sierra de Agua, 2 May 1978, Woodruff et al., 7♂, 9♀ (FSCA). **San Juan Province:** at river, 1 km off rd. to Vallejuelo, El Capá, 21 May 1985, Woodruff et al. 1♂ (FSCA).

Oxyethira (Loxotrichia) puertoricensis Flint

Oxyethira puertoricensis Flint, 1964:55 [♂, ♀, larva, case, Puerto Rico]. Flint, 1968a:40 [♂, ♀, larva, case, Jamaica]; Botosaneanu, 1991a:132 [Haiti]; Botosaneanu, 1995:32 [Dominican Republic]. *Oxyethira quelinda* Botosaneanu, 1977:267 [♂, Cuba]. Botosaneanu, 1991a:132 [Haiti]; Botosaneanu, 1995:32 [to synonymy].

This rather distinctive species has been reported from only the Greater Antilles where it is known from all four of the major islands. It has been reported from both Haiti and the Dominican Republic where it was taken in the provinces of Duarte, Independencia, La Vega, Monte Plata, and Pedernales. We have found this species quite common and can add records from the provinces of Azua, Barahona, Elías Piña, El Seibo, La Altagracia, Monseñor Nouel, Puerto Plata, San Cristóbal, and San Juan.

Material Examined.—DOMINICAN REPUBLIC. **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 7 August 1990, Rawlins et al., 5♀ (CMNH); same, but 3–4 October 1991, 2♂, 13♀ (CMNH). **Barahona Province:** San Rafael, 8.3 km S of Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 11 May 1995, Flint, 1♂ (NMNH); same, but 22 March 1999, 1♂, 2♀ (NMNH). Río Nizaito, 6 km NW Paraiso, 18°02'N, 71°12'W, 170 m, 25–26 July 1990, Rawlins &

Thompson, 8♂, 19♀ (CMNH). Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, Flint & Mathis, 2♂, 5♀ (NMNH). Confluence Río Nizaito and Río Cortico, 9.2 km NW Paraiso, 18°03'N, 71°12'W, 230 m, 9–10 August 1990, Rawlins & Thompson, 4♂, 3♀ (CMNH). **Elías Piña Province:** Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 46♂, 307♀ (FSCA). **El Seibo Province:** Pedro Sanchez, small stream, 10 June 1976, Woodruff, 1♂ (FSCA). Hotel Santa Cruz, 28 May 1985, Woodruff & Stange, 1♂ (FSCA). **Independencia Province:** La Descubierta, 3 August 1983, Woodruff, 1♀ (FSCA). Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 3♂, 4♀ (NMNH). Río Guyabal, 4.5 km N Postre Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 8♂, 4♀ (NMNH). **La Altagracia Province:** Higueral, 19 March 1985, Woodruff & Drummond, 1♂ (FSCA). **La Vega Province:** Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 10♂, 93♀ (NMNH); same, but 19–21 May 1995, 2♂, 9♀ (NMNH). Arroyo Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint, 5♂, 20♀ (NMNH). Constanza, 27 April 1978, Woodruff & Fairchild, 8♂, 6♀ (FSCA). El Convento, 12 km SE Constanza, 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 11♂, 11♀ (NMNH); same, but 6–13 June 1969, Flint & Gómez, 3♂, 7♀ (NMNH). 11.5 km S of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, Flint, 3♂, 1♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°09.9'N, 70°33.5'W, 980 m, 7 May 1995, Flint, 7♂, 8♀ (NMNH). Near mouth Arroyo Los Dajaos, 5 km SE Manabao, 19°04'N, 70°45'W, 740 m, 9 October 1991, Rawlins et al., 1♂ (CMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 1♂ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 1♂, 15♀ (FSCA). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra," along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 3♂ (FSCA). **Monseñor Nouel Province:** Hotel Jacaranda, Bonao, 27–28 June 1998, Woodruff & Baranowski, 1♀ (FSCA); same, but 18 April 2000, Woodruff & Henry, 1♂, 2♀ (FSCA). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 84♂, 132♀ (NMNH); same, but 18 March 1999, 44♂, 81♀ (NMNH); same, but 20 March 1999, 18♂, 38♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 38♂, 22♀ (CMNH). Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 11♂, 22♀ (NMNH). 20.5 km N Cabo Rojo, 12 April 2000, Woodruff & Henry, 40♂, 31♀ (FSCA). N Cabo Rojo, km 21, 1200 ft. [365 m], 1 July 1998, Woodruff & Baranowski, 2♂, 1♀ (FSCA); same, but 19 June 1976, Woodruff, 41♂, 30♀ (FSCA); same, but km 24, 3000 ft (915 m), 2 July 1998, 4♂, 3♀ (FSCA); same, but 11 June 1998, Woodruff & Freytag, 1♂, 1♀ (FSCA). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 4♂, 63♀ (NMNH). Los Hidalgos, 4–5 June 1969, Flint & Gómez, 4♂, 2♀ (NMNH). **San Cristóbal Province:** La Toma, N of San Cristóbal, 9–10 June 1969, Flint & Gómez, 2♂, 1♀ (NMNH). La Trinidad, NE Sierra de Agua, 2 May 1978, Woodruff et al., 12♂, 5♀ (FSCA). **San Juan Province:** at river, 1 km off rd. to Vallejuelo, El Capá, 21 May 1985, Woodruff et al., 15♂, 31♀ (FSCA).

Oxyethira (Dampftrichia) simulatrix Flint

Oxyethira simulatrix Flint, 1968a:43 [♂, ♀, Jamaica]. Holzenthal and Harris, 1992:174 [Costa Rica]. *Oxyethira simulatrix cubana* Kumanski, 1987:27 [♂, Cuba]. Botosaneanu, 1991a:130 [Haiti, attributed ♀ is that of *O. tegal*]; Botosaneanu and Hyslop, 1998:16 [Jamaica]. **New synonym.** *Orthotrichia* sp. Kumanski, 1987:32 [Cuba, misidentified female of *O. simulatrix*]. *Oxyethira (Dampftrichia) mirebalina* Botosaneanu. Botosaneanu, 1991a:130, fig. 56 [Haiti, ♀ allotype, is misidentified ♀ of *O. simulatrix*].

Flint has now compared topotypic examples from Jamaica with the description and figures of the subspecies *O. simulatrix cubana*. The purported differences in the tip

of lateral process of the eighth tergum, the asymmetry of the ninth sternum, and the apices of eighth sternum and claspers are all found in the types under careful inspection to agree with the condition described for *O. simulatrix cubana*. The original figures were inaccurate in these details.

The allotype female of *O. mirebalina* has been studied and compared side-by-side with known examples of *O. simulatrix* and been found identical. It is to be noted that Botosaneanu (1991a) recorded two males of *O. simulatrix* from the same locality as this female. It is unknown if the other females recorded under *O. mirebalina* are those of *O. simulatrix* or true *O. mirebalina*.

The two Cuban females recorded by Kumanski (1987) as *Orthotrichia* sp. were borrowed many years ago. Notes taken at that time state that these were a species of *Oxyethira*, either *O. simulatrix* or *O. florida*. The illustrations now look exactly like *O. simulatrix* and less like *O. florida* (see Kelley and Morse, 1982, fig. 18). The specimens may have been from the same locality as the type of *O. simulatrix cubana*, and *O. florida* was not taken by Kumanski on his trip. For these reasons we ascribe the record to *O. simulatrix*.

This species has a wide distribution on the Greater Antilles, although not yet recorded from Puerto Rico. It also is found in Central America with records from Costa Rica, but we have seen it also from Mexico and Panama. Although recorded from Haiti, these are the first records from the Dominican Republic. We have it from the Distrito Nacional and provinces of Independencia, La Altagracia, La Vega, Monte Cristi, Monte Plata, and Puerto Plata.

Material Examined.—DOMINICAN REPUBLIC. [Distrito Nacional]: Cachón de la Rubia, nr. Central Ozama, 10 June 1969, Flint & Gómez, 1♀ (NMNH). **Independencia Province:** La Descubierta, 3 August 1983, Woodruff, 1♀ (FSCA). Río Guyabal, 4.5 km N Postre Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 2♀ (NMNH). **La Altagracia Province:** La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 1♂, 25♀ (FSCA, NMNH, CMNH). Nisibón "Papagallo", 16–19 June 1998, Woodruff & Freytag, 1♀ (FSCA). Higueral, 19 March 1985, Woodruff & Drummond, 2♀ (FSCA). **La Vega Province:** Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 3♂, 5♀ (NMNH); same, but 19–21 May 1995, 5♂, 3♀ (NMNH). **Monte Cristi Province:** Monte Cristi, 4 June 1986, Miller & Stange, 19♀ (FSCA). **Monte Plata Province:** Bayaguana, 22 August–2 September 1991, Brown, 1♀ (FSCA). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 1♀ (NMNH).

HAITI. Département du Sud, Les Cayes, petit ruisseau a l'hôtel "le Relais", 30 Oct–5 Nov 1979, L. Botosaneanu, 1♀ (allotype of *O. mirebalina*) (ZMUA).

Oxyethira (Dampftrichia) tega Flint

Oxyethira tega Flint, 1968a:44 [♂, ♀, Jamaica]. Flint, 1968b:56 [♂, ♀, Dominica]; Botosaneanu, 1977:273 [Cuba].

Oxyethira (Dampftrichia) simulatrix cubana.—Botosaneanu, 1991a:130, fig. 52 [Haiti, misidentified female of *O. tega*].

The known distribution of this species is scattered across the Antilles: Cuba, Jamaica, Hispaniola, and

Dominica with the subspecies *O. tega antillarum* reported from Guadeloupe. A female of this species was reported from Haiti under the name of *O. simulatrix cubana* (this female has been studied and it is *O. tega*). We have seen two collections from La Vega and Elias Piña Provinces in the Dominican Republic.

Material Examined.—DOMINICAN REPUBLIC. **La Vega Province:** Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 19–21 May 1995, Flint, 1♂, 1♀ (NMNH). **Elias Piña Province:** Río Limpio, 2400 ft. (ca. 730 m), 26–27 Apr 2000, Woodruff & Henry, blacklight trap, 1♂, 3♀ (FSCA).

HAITI. Département du Sud, Les Cayes, petit ruisseau a l'hôtel "le Relais", 30 Oct–5 Nov 1979, L. Botosaneanu, 1♀ (ZMUA).

Oxyethira species

Oxyethira sp. Botosaneanu, 1995:29.

The unique female figured under this name has been borrowed and studied. It matches the females of none of the species recorded above. It was originally suggested as the female of *O. ortizorum*, but the females treated as *O. ortizorum* in this paper are quite different. We suspect that it represents yet another undescribed species on the island of the subgenus *Mesotrichia*, although it is possible that one of the known species has misassociated sexes. If so, then the female of that species would be an undescribed species.

Material Examined.—DOMINICAN REPUBLIC. [La Vega Province]: Cordillera Central, spring brook near Salto Agua Blanca (Convento), 11 May 1995, Botosaneanu, light, 1♀ (ZMUA).

Family Leptoceridae

Genus *Nectopsyche* Müller

This is a speciose genus limited to the New World. One or more species have been recorded from all the Greater Antillean islands, but none are known from the Lesser Antilles. The larvae have been described a number of times (Flint, 1968a; Haddock, 1977; Ross, 1944; Wiggins, 1996). They construct tubular cases utilizing many different materials, depending on the species.

Nectopsyche cubana (Banks)

Leptocella cubana Banks, 1938:299, fig. 13 [♂, Cuba]. Flint, 1967:21, fig. 99 [♂, lectotype]; Flint, 1968a:54, figs. 130, 132 [♂, ♀, Jamaica].

Nectopsyche cubana (Banks): Flint, 1992:387 [Puerto Rico, Dominican Republic]; Botosaneanu, 1996:19 [Dominican Republic].

This species has been recorded from all the Greater Antillean islands. It appears to be quite common in the Dominican Republic, being recorded from the Provinces of Azua, Dajabón, Elias Piña, El Seibo, Hato Mayor, La Altagracia, La Vega, Monseñor Nouel, Pedernales, Puerto Plata, San Juan, and Santiago.

Material Examined.—DOMINICAN REPUBLIC. **Azua Province:** Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 7 August 1990, Rawlins et al., 1♀ (CMNH). **Dajabón Province:** 9 km S Loma de Cabrera, 19°21'N, 71°37'W, 620 m, 12 July 1992, Rawlins et al., 4♂, 4♀ (CMNH). Río Massacre, Balneario Don Miguel, 7 km SW

Dajabón, 40 m, 26 May 1973, D. & M. Davis, 2♂ (NMNH). 13 km SE Loma de Cabrera, ca 400 m, 20–22 May 1973, D. & M. Davis, 1♂, 3♀ (NMNH). **Elias Piña Province:** 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 1♂, 1♀ (NMNH). Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 10♂, 17♀ (FSCA). **El Seibo Province:** Río Quisibani, E El Seibo, 18°45.3'N, 68°55.7'W, 12 May 1995, Flint, 10♂, 4♀ (NMNH). **Hato Mayor Province:** Parque Los Haitises, E of Trepada, 12 km E El Valle, 18°59'N, 69°30'W, 145 m, 6 July 1995, Rawlins et al., 5♂, 4♀ (CMNH). **La Altagracia Province:** 2 km E Nisibón, Río Nisibón, 12 June 1986, Woodruff & Stange, 3♀ (FSCA). **La Vega Province:** Near mouth Arroyo Los Dajaos, 5 km SE Manabao, 19°04'N, 70°45'W, 740 m, 9 October 1991, Rawlins et al., 30♂, 2♀ (CMNH). La Ciénega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 2♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 1♂, 8♀ (FSCA). 5 km W Manabao, Finca Eliado Fernandez "Paso la Perra," along Río Yaque del Norte, 3050 ft [ca. 930 m], 19–23 April 2000, Woodruff & Henry, 8♂, 35♀ (FSCA); same, but 15 May 2001, Woodruff & class, 11♂, 3♀ (FSCA). 2.5 km SW Piñar Bonito, 18°51'N, 70°43'W, 1430 m, 26 November 1992, Rawlins et al., 1♂, 4♀ (CMNH). Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 18♂, 7♀ (NMNH); same, but 19–21 May 1995, 11♂, 4♀ (NMNH). Río Baiguate, Bamboo Hole Canyon, 5 km SE Jarabacoa, 580 m, 22 July 1987, Rawlins & Davidson, 1♀ (CMNH). Salto Guasara, 9.5 km W Jarabacoa, 19°04.4'N, 70°42.1'W, 680 m, 19 May 1995, Flint & Mathis, 14♀ (NMNH). Jarabacoa, 3–4 June 1969, Flint & Gómez, 3♂, 1♀ (NMNH); same, but 13 November 1984, Spangler & Faitoute, 3♂, 1♀ (NMNH). Río Camú, 19 km NE Jarabacoa, 12 June 1969, Flint & Gómez, 2♂, 2♀ (NMNH). Arroyo La Palma, 9.5 km E El Río, 19°0.9'N, 70°33.5'W, 980 m, 7 May 1995, Flint, 1♀ (NMNH). La Palma, 12 km E of El Río, 2–13 June 1969, Flint & Gómez, 1♂ (NMNH). Convento, 12 km SE Constanza, 6–13 June 1969, Flint & Gómez, 7♂, 21♀ (NMNH); same, but 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 8♂, 4♀ (NMNH). **Monseñor Nouel Province:** Bonao, Hotel Jacaranda, 27–28 June 1988, Woodruff & Baranowski, 1♀ (FSCA). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 10♂, 1♀ (NMNH); same, but 18 March 1999, Flint, 4♂, 3♀ (NMNH); same, but 20 March 1999, 1♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 25♂, 21♀ (CMNH). **Puerto Plata Province:** Río Camú, 14 km E Puerto Plata, 19°11.9'N, 70°37.4'W, 20 m, 17 May 1995, Flint, 1♂, 4♀ (NMNH). [**San Cristobal Province:** at or near Naranjo Dulce, 13 km N San Cristobal]: S. Francisco Mts., Sept 1905, Aug. Busck, 2♀ (NMNH). **San Juan Province:** at river, El Capá, 21 May 1985, Woodruff et al., 1♀ (FSCA). **Santiago Province:** 1 km NE San José de las Matas, 19°21'M, 70°56'W, 540 m, 11 July 1992, Rawlins et al., 1♀ (CMNH).

Genus *Oecetis* McLachlan

This is a large and diverse genus that is found in all regions of the world, except the polar. It seems to be able to disperse readily to isolated islands, including many in the Pacific. The immature stages of many species have been described (Flint, 1968b; Ross, 1944; Wiggins, 1996). They all construct portable, tubular cases, mostly of plant material, but some species groups use small sand grains.

Oecetis inconspicua (Walker)

Leptocerus inconspicua Walker, 1852:71 [U.S.A.].

Oecetis inconspicua (Walker): Betten and Mosely, 1940:67, fig. 32 [♂, redescription of type]; Flint, 1964:64, figs. 17A–B [♂, ♀, Puerto Rico]; Flint, 1968a:54, figs. 128, 129 [♂, ♀, Jamaica]; Botosaneanu, 1991a:134 [Haiti].

O. inconspicua is a very common species widely distributed in the New World. On the continent it is

known from Canada south through North and Central America into northern South America, at least. It has been recorded from all the Greater Antillean islands and Trinidad, but none of the other Lesser Antillean islands. It does not seem abundant on Hispaniola, but may be fairly widely distributed: Barahona, Independencia, La Vega and Monte Cristi Provinces, and the Departement de l'Ouest in Haiti.

Material Examined.—**DOMINICAN REPUBLIC.** **Barahona Province:** 24 km E Barahona, 27 September 1985, Woodruff & Stange, 1♂ (FSCA). 5 km NW Barahona, Agr. Exp. Station, 29–30 April 1978, Woodruff et al., 1♂, 4♀ (FSCA). **Independencia Province:** Río Las Damas, 2 km S Duvergé, 18°22.0'N, 71°31.4'W, 10 m, 24 March 1999, Flint, 2♂, 2♀ (NMNH). Río Guyabal, 4.5 km N Postre Río, 18°34.7'N, 71°37.7'W, 150 m, 25 March 1999, Flint, 1♂, 1♀ (NMNH). **La Vega Province:** Jarabacoa, 3–4 June 1969, Flint & Gómez, 2♀ (NMNH). Río Camú, 19 km NE Jarabacoa, 12 June 1969, Flint & Gómez, 1♀ (NMNH). Río Baiguate, 1–2 km S Jarabacoa, 19°06.9'N, 70°37.0'W, 520 m, 8–9 May 1995, Flint, 1♀ (NMNH). **Monte Cristi Province:** 10 km S Monte Cristi, 5 m, 23 May 1973, D. & M. Davis, 1 w/o abdomen (NMNH).

HAITI. [Département de l'Ouest]: Manneville, 16–17 November 1934, Darlington, 1♀ (MCZ).

Oecetis haitises Flint and Sykora, new species (Fig. 30)

A single female is known from Hato Mayor Province that is clearly different from the preceding species. At first it was believed to be *O. pratti* Denning, but comparison with material of *O. pratti* showed it lacks the black spots on the wings present in *O. pratti*. When the abdomen was cleared, the genitalia were seen to be abundantly distinct from those of *O. pratti*. The only other Greater Antillean *Oecetis* is *O. maspeluda* Botosaneanu, described from Cuba. Study of its types shows it to be virtually identical to *O. pratti*, except for its more strongly developed scent hairs on the male hind wing. The female genitalia appear inseparable from those of *O. pratti*. Thus, no species currently known from the Antilles is the same as our Hispaniolan example, nor does it seem likely that this is a continental species.

In comparison with *O. pratti*, *O. haitises* lacks all wing markings, the lateral lobe of the ninth segment is downturned at its apex, the tenth segment is undeveloped, and the anterior margin of internal sac is deeply indented mesally.

Adult Male.—Unknown.

Female.—Length of forewing, 6 mm. Color stramineous, unmarked. Genitalia: Ninth segment broad laterally, dorsally slightly overhanging, with pair of small knob-like protuberances; lateroventral lobe as long as high, apex decurved. Cercus protruding, broad in both lateral and dorsal aspects. Tenth segment undeveloped. Vaginal sclerites shield-shaped, with elongate posterolateral supports; with central opening and long, tongue-like lobe. Internally with heavily sclerotized structure (probably connected to vaginal sclerite by membrane); almost spherical in lateral aspect with anterior half darkened, in

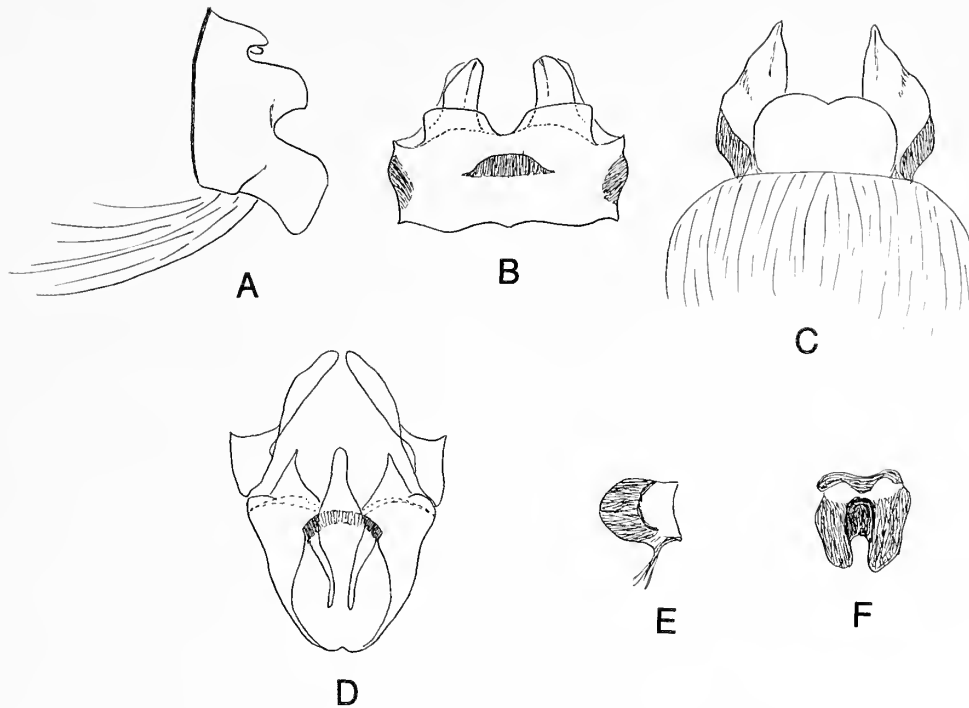


Fig. 30.—*Oecetis haitises* new species, female genitalia: A, Lateral. B, Dorsal. C, Ventral. D, Vaginal sclerites, ventral. E, Sclerotized vaginal structure, lateral. F, Same, ventral.

ventral aspect with lateral lobes, and deep anteromesal sinus.

Type Material.—Holotype, female: **DOMINICAN REPUBLIC**. **Hato Mayor Province**: Parque Los Haitises, 3 km W Cueva de Arena, 19°04'N, 69°29'W, 20 m, 7–9 July 1992, J. Rawlins, R. Davidson, S. Thompson, C. Young, mesic lowland forest (CMNH).

Genus *Setodes* Rambur

This is a genus widely distributed in the world, and extremely diverse in southern Asia (Schmid, 1987). It is notably absent in New Zealand, western North America and all of Central and South America. Heretofore it was unknown from the Antilles except for two species found in Dominican amber (Wichard, 1995b). The following species is included in *Setodes* with some hesitation as it seems rather aberrant, but no other described genus seems more appropriate. The larvae of several species have been described (Wiggins, 1996; Yang and Morse, 1989). They construct very solid, cylindrical and slightly curved, sand grain cases. They appear to burrow into the substrate, often in fine sand found in the lee of rocks.

Setodes anomalus Flint and Sykora, **new species** (Fig. 31)

As its specific epithet implies, this species is hard to place in the body of the genus, in spite of its recent revision by Schmid (1987). The apparent lack of parameres and presence of a sclerite between the tenth tergum and preanal

appendages are very uncommon in the genus. The venation is within the bounds of variation, although the discoidal cell is extremely long and the crossveins are unnoticeable. The situation with the mesokatepisternum and epicranial sutures (see Ross, 1944 p. 21) is also variable. Examples of various species from around the world shows that the mesokatepisternum may be truncate or pointed, and epicranial sutures may be present or absent in various combinations. The male genitalia are very distinctive with the elongate preanal appendage, presence of a sclerotized plate between the tenth tergum and preanal appendage, knob-like inferior appendage with two appendages, and simple tubular phallus with parameres reduced to darkened structures appressed to the phallosome. The female is also distinctive with its elongate preanal appendage, fusion of the tenth tergum to the lamella, and structure of the vaginal sclerites.

Adult Male.—Length of forewing 6 mm. Color in alcohol, brown; forewing brown with indications of darker maculae. Epicranial and lateral sutures of head present, epicranial stem about as long as anterior arms. Forewing discal cell extending to 60% distance from apex to base of wing; crossveins not apparent except sectoral crossvein closing discal cell, which appears very oblique. Mesokatepisternum elongate, truncate dorsally. Spurs 0,2,2. Genitalia: Ninth segment broad, anterior and posterior margins parallel. Preanal appendage elongate, clavate. Tenth tergum declivous tapering apicad in lateral aspect, deeply divided mesally in dorsal aspect; lateral sclerite of

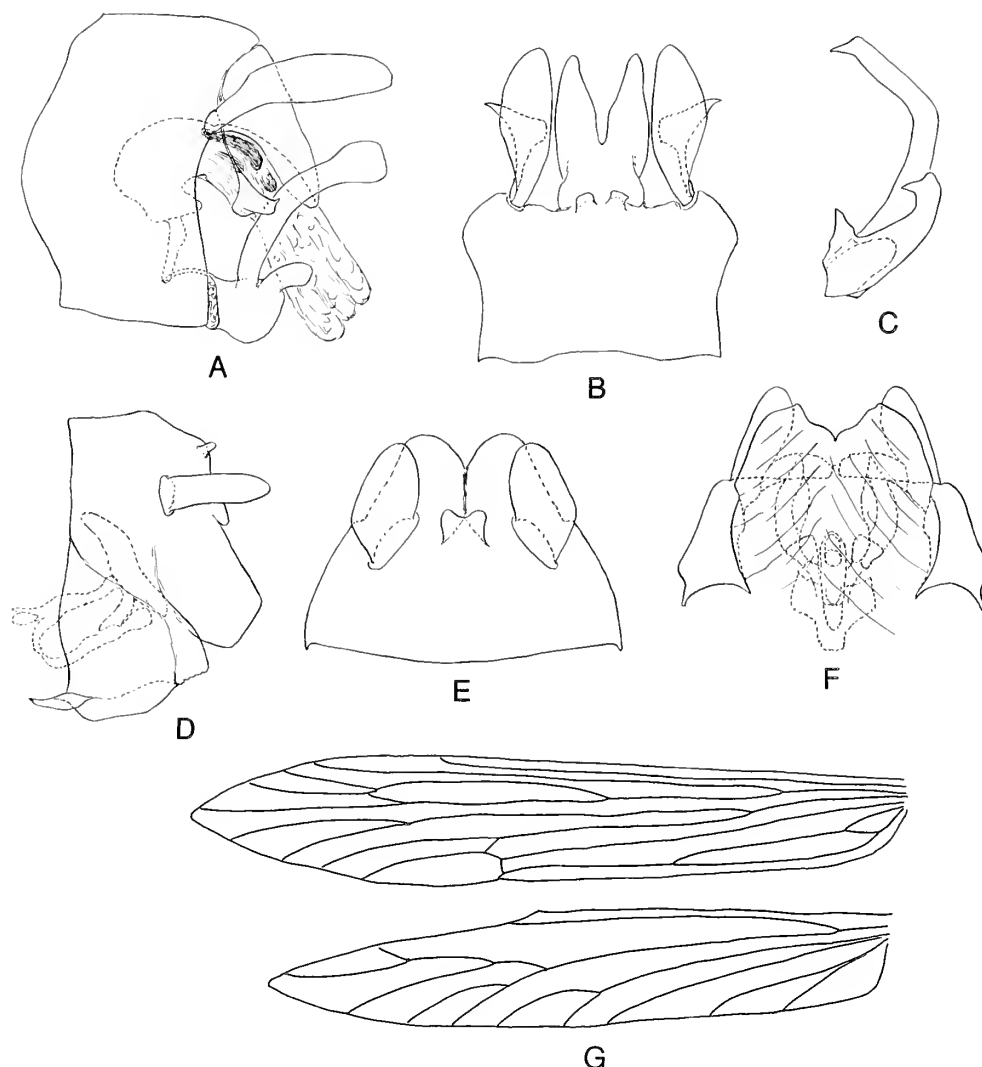


Fig. 31.—*Setodes anomalus* new species, male genitalia: A, Lateral. B, Dorsal. C, Inferior appendage, posteroventral. Female genitalia: D, Lateral. E, Dorsal. F, Ventral. Wing venation: G, Dorsal.

tenth tergum present, with its apex strongly sclerotized and directed ventrolaterad. Inferior appendage spherical basally, with two dorsal processes; apical one terete about twice as long as wide, dorsal one terete, ten times as long as broad; in posterior aspect base with acute apex directed caudad and each process ending in triangular point directed mesad. Phallus tubular, angled posteroventrad beyond base, apex membranous; at curve, with paired dorsal, dark structures appressed to phallosome.

Female.—Length of forewing, 6 mm. Color and structure as in male. Genitalia: Ninth segment broad, anterior margin vertical in lateral aspect. Preanal appendage elongate, depressed. Tenth tergum with pair of small processes basomesally, fused to dorsal surface of lamellae. Lamella broad, apex obliquely truncate, angled posteroventrad, apex emarginate mesally in dorsal aspect. Gonopod plate lightly sclerotized, posterior margin

slightly bilobate; junction of lateral margin and ninth segment developed as thin, overhanging ridge. Vaginal sclerites complex; central elongate structure with opening, lateral wings convoluted and sclerotized and pair of posterior supporting bands.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC, Peravia Province**: 3 km SW La Nuez, tributary to Río Las Cuevas, 18°40'N, 70°36'W, 1870 m, 5–6 August 1990, J. Rawlins & S. Thompson (CMNH). Paratypes: Same data, 1♂, 1♀ (CMNH, NMNH). **La Vega Province**: 8 km SE Constanza, near Valle Nuevo, 18°50'N, 70°42'W, 1930 m, 17 August 1990, J. Rawlins & S. Thompson, 1♂ (CMNH).

Family Odontoceridae
Genus *Marilia* Müller

The genus was originally described from the New World, where it is widely distributed, but is now known

from southern Asia and Australia. Its distribution is irregular in the Antilles, being found on Cuba, Jamaica and Hispaniola but not again till Trinidad. The larvae have been described a number of times (Flint, 1968a; Wiggins, 1996). The larvae live in lotic waters, and construct rigid, slightly curved, tubular cases of sand grains.

Marilia gracilis Banks

Marilia gracilis Banks, 1938:297, figs. 9, 21 [♂]. Flint, 1967:19, figs. 110, 111 [♂, lectotype].

This species is still known from only the type series collected in the Massif De La Selle. The basal segment of the inferior segment is noticeably longer and distinctly constricted at midlength in both lateral and posterior aspects and the apical segment is also proportionately longer and more curved than these segments are in *M. nigrescens*. We believe these differences are sufficient to merit recognition of these two forms as full species.

Material Examined.—HAITI. [Département de l'Ouest]: La Visite & vic., La Selle Range, 5–7000 ft. [1525–2135 m], Sept. 16–23 1934, M. Bates, ♂ holotype, 4♂ paratypes (MCZ).

Marilia nigrescens Banks, new status

Marilia gracilis var. *nigrescens* Banks, 1941:397.

Marilia gracilis nigrescens Banks: Flint, 1967:20, fig. 112 [♂, lectotype].

This species appears limited to the Cordillera Central in the Dominican Republic. It is virtually identical to *M. gracilis*, except that it is noticeably darker in coloration. The male genitalia of the two species differ slightly, especially in the basal segment of the inferior appendage which is shorter and tapers more regularly from base to apex in both lateral and posterior aspects and the apical segment that is not as strongly curved and proportionately shorter.

Material Examined.—DOMINICAN REPUBLIC. [La Vega Province]: Valle Nuevo, SE Constanza, c. 7,000 ft. [2135 m], Aug. '38, Darl.[ington], ♂ holotype, 1♂, 1♀ paratypes (MCZ). **Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°39'N, 70°36'W, 1880 m, 5–6 October 1991, J. Rawlins et al., 5♂, 1♀ (CMNH, NMNH); same, but 5–6 August 1990, 23♂, 3♀ (CMNH, NMNH, FSCA). [Santiago Province]: Valle de Bao, 5885 ft. [ca. 1795 m], 9 July 1992, Ivie, 1♀ (NMNH).

Marilia valga Flint and Sykora, new species
(Fig. 32)

On the basis of the male genitalia, this new species is closely related to *M. gracilis*. The coloration of the two species seems to be identical, but *M. valga* is smaller, forewing length 10 mm as opposed to 12–13 mm and the eyes are even closer dorsomesally. The mesal margin of the basal segment of the inferior appendage is strongly bent and the apical segment is even proportionately longer than these are in *M. gracilis*. Females of this species have been taken at widely scattered localities from near sea level to nearly 1900 meters elevation. This sex may be distin-

guished from that of *M. nigrescens* (the female of *M. gracilis* is unknown) by the ventral end of the ninth tergum: in *M. valga* it widens ventrad, with the end truncate, but in *M. nigrescens* it tapers to a sharp point.

Adult Male.—Length of forewing 10 mm. Color pale gray with darker maculae; hair of head, thorax and scape, hoary; flagellar segments dark with small, white ring; forewing pale gray irregularly maculate with dark gray, especially near chord. Eyes very large with very narrow furrow separating them middorsally. Spurs 2,4,4. Genitalia: Ninth segment with anterior margin concave for dorsal quarter, nearly vertical beneath; dorsal and ventral braces almost horizontal and parallel. Cercus elongate, slender, barely widened apicad. Tenth tergum with apex slightly angled, apicoventral angle strongly sclerotized, hooked lateroventrad. Inferior appendage slightly inflated basally in lateral aspect, in posterior aspect with base much widened, then sharply constricted for apical half; apical segment long, slender, curved mesad, surface with scattered rugosities. Phallus curved basally, phallosome with distinct cross band at midlength; phallosomal sclerite C-shaped with dorsal and ventral ends enlarged in lateral aspect, outer surface of endotheca rather strongly sclerotized.

Female.—Length of forewing, 8–10 mm. Color as in male. Genitalia: Eighth sternum with lateral portion produced and rugose. Ninth tergum ventrally widened, with small, anteroventral lobe, indented in dorsal or ventral aspects.

Type Material.—Holotype, male: DOMINICAN REPUBLIC. **Peravia Province:** 3 km SW La Nuez, upper Río Las Cuevas, 18°40'N, 70°36'W, 1850 m, cloud forest on river, 5–6 August 1990, J. Rawlins & S. Thompson (CMNH). Paratypes: Same data, 12♀ (CMNH, NMNH); same, but tributary to Río Las Cuevas, 1870 m, 1♀ (CMNH); same, but 18°39'W, 70°36'W, 1880 m, 5–6 October 1991, cloud forest on river, Rawlins et al., 2♀ (CMNH). [La Vega Province]: Convento, 12 km S of Constanza, 6–13 June 1969, Flint & Gómez, 1♀ (NMNH). **La Altagracia Province:** Río Nisibón, 2 km E Nisibón, 12 June 1986, Woodruff & Stange, 1♀ (FSCA).

Family Philopotamidae
Genus *Chimarra* Stephens

This is a very large genus, widely distributed over most of the world, but most speciose in tropical and subtropical regions. Blahnik (1998) listed 94 species of the subgenus *Chimarra* from the Neotropical region. The subgenus *Chimarrita* contains 18 species (Blahnik, 1997), the subgenus *Curgia* contains 92 species (Flint, 1998), and the remaining subgenus, *Otarra* contains 31 species and subspecies (Blahnik, 2002). In the Old World nearly 400 species are known, but all are currently placed in the subgenus *Chimarra*. The subgenus *Chimarra* is lacking from the Greater Antilles, whereas the subgenus *Chimarrita* is lacking from the Lesser Antilles. Larvae, pupae and their nets and general habits are well known (Wallace and Malas, 1976; Wiggins, 1996). Wichard (1983a, 1983b) described five species from Dominican amber.

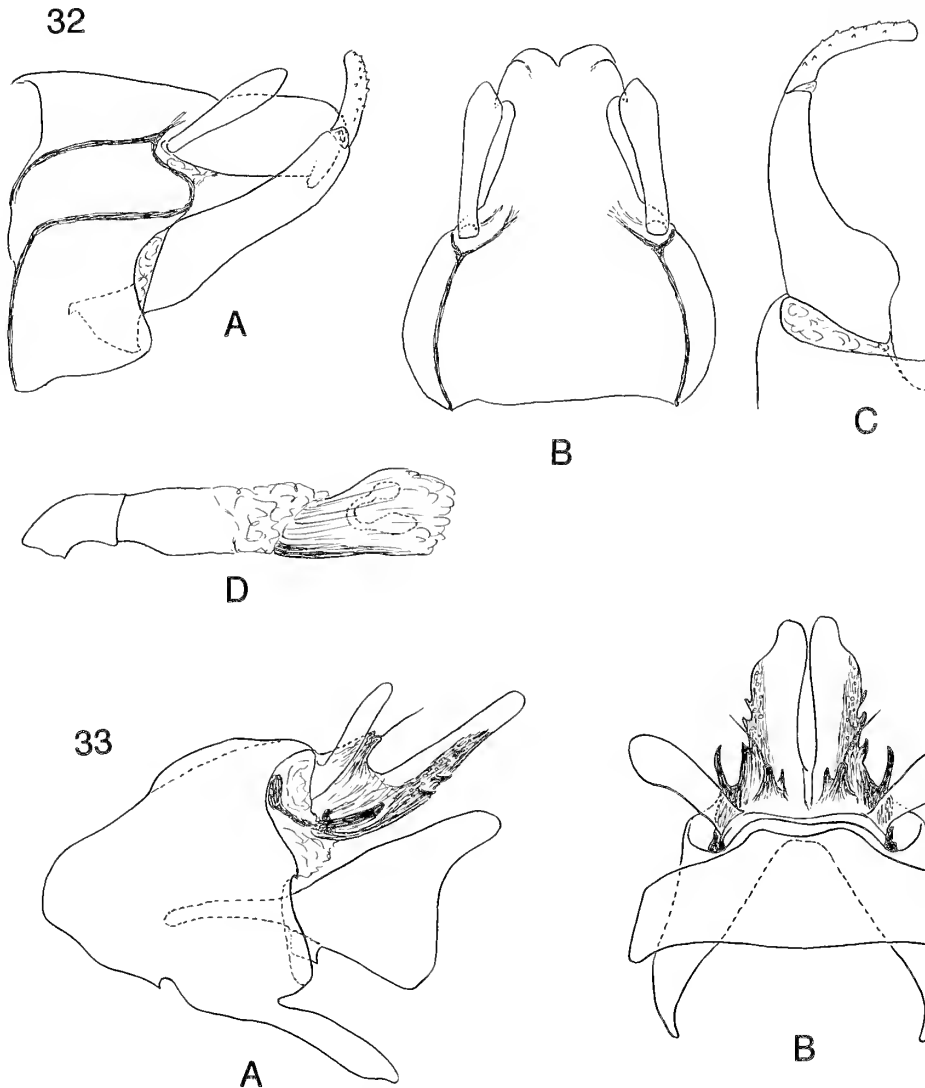


Fig. 32.—*Marilia valga* new species, male genitalia: A, Lateral. B, Dorsal. C, Inferior appendage, posteroventral. D, Phallus, lateral.

Fig. 33.—*Chimarra (Otarra) spinulifera baoruco* new subspecies, male genitalia: A, Lateral. B, Dorsal.

Chimarra (Curgia) braconoides (Walker)

Curgia braconoides Walker, 1860:179.

Chimarra braconoides (Walker): Betten and Mosely, 1940:15, fig. 7 [redescription of holotype].

Chimarra (Curgia) braconoides (Walker): Flint, 1998:52, figs. 1–5, 228–232 [redescription, Dominican Republic, Haiti].

This is the first caddisfly described from the island of Hispaniola. It is closely related to *Ch. (Cu.) gilvimacula*, but can be distinguished by coloration—the pale marks on the forewing are larger and deep orange, rather than narrow and yellowish—and in the structure of the male genitalia. Extensive records of the species were given by Flint (1998), and the few new records that are available add only Barahona Province. It has been recorded from the provinces of Baoruco, Dajabón, El Seibo, Hato Mayor, Elias Piña, La Vega, Pedernales,

San Cristóbal, Santiago, and the Distrito Federal as well as Haiti.

Material Examined.—DOMINICAN REPUBLIC. **Barahona Province:** Río Nizaito, 5 km N Paraiso, 18°01.5'N, 71°11.6'W, 150 m, 21 March 1999, Flint, 2♀ (NMNH). **Pedernales Province:** Río Mulito, 21 km N Pedernales, 280 m, 18°09.3'N, 71°45.6'W, 20 March 1999, Flint, 1♀ (NMNH). Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint, 2♀, plus 1♂ metamorphotype (NMNH).

Chimarra (Curgia) gilvimacula Flint

Chimarra (Curgia) gilvimacula Flint, 1998:52, figs. 233–236 [♂]. Botosaneanu, 1996:12 [Dominican Republic].

Chimarra braconoides (Walker) or *gilvimacula* Flint: Botosaneanu, 1996:12 [unidentified females].

This species, only recently described, is very closely related to *Ch. (Cu.) braconoides*. It is most easily

recognized by the paler, yellowish maculae on the forewings. It was recorded from the provinces of Azua, Dajabón, Duarte, El Seibo, Elías Piña, Hato Mayor, La Vega, Pedernales, Puerto Plata, San Cristóbal, San Juan, as well as Haiti. The new material currently available, here listed, adds only the Province of La Altagracia to its known distribution.

The unidentified female specimens mentioned by Botosaneanu (1996) from the Provinces of La Vega, Duarte and Pedernales have been examined. There is enough of the colored hair left on the wings, even though they are preserved in alcohol, to make a reasonably reliable determination that they are all *Ch. gilvamacula*.

Material Examined.—DOMINICAN REPUBLIC. [Duarte Province]: Cord. Septentrional, Loma Quita Espuela, Arroyo Los Guineos, 27 April 1995, L. Botosaneanu, light, 1♀ (ZMUA). [Elías Piña Province]: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 46♂, 50♀ (FSCA). [El Seibo Province]: Pedro Sánchez, small stream, 10 June 1976, Woodruff, 9♂, 25♀ (FSCA, NMNH). [La Altagracia Province]: La Laguna Nisibón at Río Maimón, 18 June 1998, Woodruff & Freytag, 2♂, 2♀ (FSCA). 2 km E Nisibón, Río Nisibón, 12 June 1986, Woodruff & Stange, 62♂, 36♀ (FSCA, NMNH). Nisibón, Finca Papagallo, 16–19 June 1999, Woodruff & Baranowski, 1♂ (FSCA); same, but 4–8 April 2000, Woodruff & Henry, 3♂, 9♀ (FSCA, NMNH). [La Vega Province]: Cord. Central, Jarabacoa, Salto de agua Bayaguata, 10 May 1995, L. Botosaneanu, at light, 1♀ (ZMUA). [Monseñor Nouel Province]: Bonao, Río Yuna, 600 ft [ca. 180 m], 18 April 2000, Woodruff & Henry, 1♂ (FSCA). [Pedernales Province]: Río Mulito, 21 km N Pedernales, 270 m, 18°09.3'N, 71°45.6'W, 18 March 1999, Flint, 9♂, 17♀, plus 17 larvae, 1 prepupa, 1 pupa, 1♂ pupa (NMNH); same, but 20 March 1999, 6♂, 8♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 7♂, 1♀ (CMNH). Stream & falls, 19 km N Pedernales, 18°09.2'N, 71°44.8'W, 230 m, 19 March 1999, Flint & Mathis, 12♂, 20♀, plus 1 larva, 1 pupa, 1♂ metamorphotype (NMNH). Spring La Aguita, ca. 1.5 km from Mulito to Pedernales, 5 May 1995, L. Botosaneanu, 3♀ (ZMUA). [San Cristóbal Province]: La Trinidad, NE Sierra de Agua, 2 May 1978, Woodruff et al., 10♂, 5♀ (FSCA).

Chimarra (Chimarrita) merengue Blahnik

Chimarra (Chimarrita) merengue Blahnik, 1997:210, figs. 4A–E, G, H [♂, ♀].

This species is closely related to *Ch. (Ci.) maldonadoi* from Puerto Rico; the two seem to be rather systematically isolated from all other species in the subgenus. Originally described from a few specimens taken in the province of Dajabón, *C. merengue* is now recorded from the Provinces of La Vega and Monseñor Nouel.

Material Examined.—DOMINICAN REPUBLIC. [Dajabón Province]: 1.3 km S Loma de Cabrera, 400 m, 20–22 May 1973, D. & M. Davis, ♂ holotype, 1♂, 3♀ paratypes (NMNH). [La Vega Province]: 5 km SSE Jarabacoa, 640 m, 25 July 1987, J.E. Rawlins, 1♂ (CMNH). Near mouth Arroyo Los Dajos, 5 km E Manabao, 19°04'N, 70°45'W, 740 m, 9 Oct 1991, Rawlins et al., 1♀ (CMNH). Bayacanes, 120 m, 24 July 1987, Rawlins & Davidson, 1♂ (CMNH). [La Vega-Monseñor Nouel Provinces]: Loma el Casabito, summit, 19°03'N, 70°31'W, 1390 m, 19–23 November 1992, Rawlins et al., 3♀ (CMNH, NMNH).

Chimarra (Otarrrha) koki Botosaneanu

Chimarra koki Botosaneanu, 1996:11, figs. 7–12 [♂, ♀]. Blahnik, 2002:85 [relationships].

This recently described species is known from only a few localities in the Cordillera Central in the Provinces of La Vega, Monseñor Nouel and now Peravia.

Material Examined.—DOMINICAN REPUBLIC. [Monseñor Nouel Province]: nr. Jima [on road to Constanza], 670 m, 19°01.2'N, 70°28.8'W, 6 May 1995, Flint, 3♂, 1♀ paratypes. [Peravia Province]: tributary to upper Río Las Cuevas, 3 km SW La Nuez, 18°40'N, 70°36'W, 1870 m, 5–6 August 1990, Rawlins & Thompson, 2♂ (CMNH, NMNH).

Chimarra (Otarrrha) redonda Blahnik

Chimarra redonda Blahnik, 2002:98, figs. 25, 47 [♂, ♀]. Botosaneanu, 1996:11 [Dominican Republic].

This species has been formally described only recently, but its identity was known through the unpublished thesis of its author since 1996. The few records are from La Vega Province.

Material Examined.—DOMINICAN REPUBLIC. [La Vega Province]: La Palma, 12 km E El Río, 2–13 Jun 1969, Flint & Gomez, ♂ holotype, 16♂, 8♀ paratypes (NMNH).

Chimarra (Otarrrha) spinulifera spinulifera Flint

Chimarra (C.) spinulifera Flint, 1968c:151, figs. 4–7 [♂]. Botosaneanu, 1996:11 [Dominican Republic]; Blahnik, 2002:107, fig. 31, [♂, redescription].

This, the nominotypic subspecies, is still known from only the unique holotype taken near the southwestern tip of Haiti.

Material Examined.—HAITI. [Département du Sud]: Roche Croix, Mt. La Hotte, 4000 ft [ca. 1200 m], 14 Oct 1945, Darlington, ♂ holotype (MCZ).

Chimarra (Otarrrha) spinulifera galalcha Botosaneanu

Chimarra spinulifera galalcha Botosaneanu, 1996:11, figs. 13–18 [♂, ♀]. Blahnik, 2002:107, figs. 32, 50 [♂, ♀, redescription, Dominican Republic].

This is the form (species or subspecies?) of *C. spinulifera* that inhabits both the Cordilleras Central and Septentrional in the Dominican Republic. It can be rather common in some areas around Jarabacoa in the central highlands. The recorded material is from the Provinces of La Vega, Duarte, and Elías Piña.

Material Examined.—DOMINICAN REPUBLIC. [Elías Piña Province]: 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 2♂, 6♀ (NMNH). [La Vega Province]: Arroyo Guasara, 9.5 km W Jarabacoa, 680 m, 19°04.4'N, 70°42.1'W, 19 May 1995, Flint, 14♂, 2♀ paratypes (NMNH). Río Baiguata, 1–2 km S Jarabacoa, 520 m, 19°06.9'N, 70°37.0'W, 8–21 May 1995, Flint, 41♂, 56♀ paratypes (NMNH). 5 km S Jarabacoa [on road to El Río], 640 m, 19°05.8'N, 70°36.5'W, 8–20 May 1995, Mathis, 1♂ paratype (NMNH).

Chimarra (Otarrrha) spinulifera baoruco Flint and Sykora, new subspecies (Fig. 33)

Chimarra spinulifera spinulifera Flint: Botosaneanu, 1996:12 [Dominican Republic].

The nominotypic subspecies was described from a unique male from Mt. La Hotte in extreme southwestern Haiti. The subspecies *Ch. s. galalcha* was described by Botosaneanu (1996) from the Cordillera Central and the Loma Quita Espuela in Duarte Province. This new subspecies is known from only a small, spring-fed brook arising from the base of the Sierra de Baoruco. Except for the subspecies *Ch. s. galalcha*, which is known from a number of localities and in good numbers, the other subspecies are each known from only one or a few specimens from a single site. Additional material from other sites, especially the other mountain ranges, and longer series may show all to be a single, variable species, or may substantiate the validity of the various subspecies.

The differences among the three subspecies seems to lie wholly in the ornamentation of the tenth tergum of the male. In the nominotypic subspecies the tenth tergite bears a long, basolateral spine and another long spine, with a few shorter basomesal spinelets. In *Ch. s. galalcha* the basolateral spine is much shorter and the basomesal spine is reduced to a low, rounded knob. The subspecies *Ch. s. baoruco* again bears a long basolateral spine, but the basomesal spine is noticeably elongate, bifid or even multifid apically with the points variable in length. The females of the last two subspecies do not offer any clear-cut genitalic differences.

Adult Male.—Length of forewing, 3.5–4 mm. Color fuscous, immaculate. Genitalia: Eighth tergum slightly and broadly produced posteromesad. Ninth segment rounded anteriorly; with long, terete ventromesal process. Tenth tergite with long, basolateral spine and with elongate, basodorsal process bifid apically; lateral margin with several short spines; in dorsal aspect deeply divided mesally with lateral margin heavily sclerotized, mesally more membranous. Cercus large, earlike, flared laterad. Inferior appendage trianguloid in lateral aspect with apicodorsal extension broad in lateral aspect but slender in ventral. Phallus with phallosome slender, straight; phallosomal sclerites elongate, complex, lightly sclerotized.

Female.—Length of forewing, 4 mm. Color as in male. Genitalia: Eighth segment lacking anterolateral apodemes, deeply divided ventrolaterally; ventromesally with broad, truncate lobe. Ninth tergite with long, slender ventrolateral apodeme. Vaginal sclerites lightly sclerotized, inconspicuous.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC.** Barahona Province: San Rafael, 8.3 km S Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 22 March 1999, Flint (NMNH). Paratypes: Same data, 2♂, 1♀ (NMNH, CMNH); same, but, 15 May 1995, 1♀ (NMNH). S. de Baoruco, Arroyo San Rafael, 5 Apr 1995, L. Botosaneanu, light, 1♂ (ZMUA).

Family Polycentropodidae
Genus *Antillopsyche* Banks

This is the only known New World genus belonging to the subfamily Pseudoneureclipsinae, which is otherwise

known only from the Old World tropics. Two species are known from Cuba, one from Puerto Rico, and one extant species from the Dominican Republic. In addition, the species *A. oliveri* Wichard (1985) is the most frequently encountered caddisfly in Dominican amber. The larva, pupa, and retreat were described for the Puerto Rican *A. tubicola* (Flint, 1964).

Antillopsyche demma Botosaneanu

Antillopsyche demma Botosaneanu, 1996:13, figs. 22–26 [♂].

Although presently known from only the Dominican Republic, it has been taken close to the Haitian border near Pedernales. It is known from the Provinces of Dajabón, Elias Piña, Hato Mayor, Pedernales, and La Vega as well as the site, “S. Francisco Mts.” in San Cristobal Province.

Material Examined.—**DOMINICAN REPUBLIC.** Dajabón Province: 13 km S Loma de Cabrera, ca. 400 m, 20–22 May 1973, D. & M. Davis, 1♀ (NMNH). Elias Piña Province: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 4♀ (FSCA). Hato Mayor Province: Parque Los Haitises, E of Trepada Alta, 12 km W El Valle, 18°59'N, 69°30'W, 145 m, 6 July 1992, Rawlins et al., 1♂, 4♀ (CMNH). La Vega Province: Jarabacoa, 3–4 June 1969, Flint & Gómez, 3♀ (NMNH). Bayacanes, 120m, 24 July 1987, Rawlins & Davidson, 1♂ (CMNH). Pedernales Province: Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 1♀ (NMNH); same, but 18 March 1999, 4♂, 7♀ (NMNH); same, but 20 March 1999, 1♂, 15♀ (NMNH); same, but 13 km N Pedernales, 18°09'N, 71°46'W, 17 July 1992, 230 m, Rawlins et al., 45♂, 36♀ (CMNH, FSCA). Km 21, N Cabo Rojo, 1200 ft [365 m], 19 June 1976, Woodruff, 1♀ (FSCA). [San Cristobal Province: at or near Naranjo Dulce, 13 km N San Cristobal], S. Francisco Mts., Sept 1905, Aug. Busck, 3♂ paratypes, 2♀ (NMNH).

Genus *Cerutina* Ross

The genus is found throughout the New World from the northern United States south to the Río de la Plata. It has been found on all the Greater and some of the Lesser Antillean islands. A single species is known from Hispaniola and the genus has been recorded also from Dominican amber (Wichard, 1987). The larva of the Puerto Rican *C. mastelleri* Flint was described (Flint, 1964) as Polycentropodinae species.

Cerutina danieli Flint and Sykora, new species
(Fig. 34)

Cerutina sp. Flint & Perez-Gelabert, 1999:43 [erroneously listed as ♂, recte ♀].

This uncommon species is closely related to the Jamaican *C. caliginosa* Flint and more distantly to the Puerto Rican *C. mastelleri* Flint. With both it shares the absence of the dorsal process of the inferior appendage and with *C. caliginosa* it agrees in the shape of the intermediate and inferior appendages. There are small but distinct differences between the two in the exact contour of the inferior appendages, but the primary differences are seen in the ventromesal lobes of the intermediate appendages. In ventral aspect this lobe is

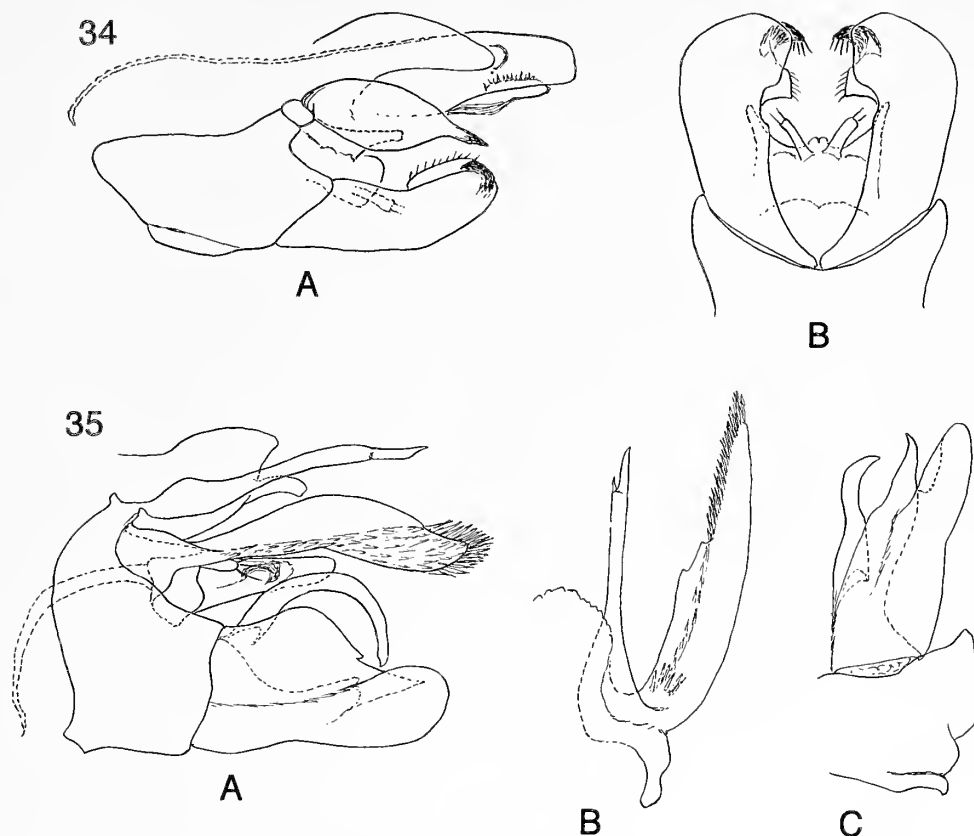


Fig. 34.—*Cernotina danieli* new species, male genitalia: A, Lateral. B, Ventral.

Fig. 35.—*Polycentropus pedernales* new species, male genitalia: A, Lateral. B, Tenth tergum and preanal appendage, dorsal. C, Ninth sternum and inferior appendage, ventral.

truncate with a small mesal cleft in *C. caliginosa*, but in *C. danieli* this lobe bears two pairs of processes, one submesally the other posterolaterally. The female described here is associated with the male based purely on supposition. But its genitalia are virtually identical to those of the Jamaican species (see Flint, 1968a, fig. 36), as would be expected based on the similarity of the males.

Adult Male.—Length of forewing, 4.5 mm. Color brown in alcohol. Genitalia: Ninth segment with anterior margin produced anteriad, rounded. Tenth tergum elongate, membranous, divided dorsomesally. Preanal appendage wide basally, tapering abruptly to darkened, narrow, pointed apex directed mesad; ventromesal lobe bearing pair of dorsolateral processes, pair of ventromesal, tubular processes, and mesal lobe, rounded in lateral aspect. Inferior appendage lacking basodorsal lobe; with apicodorsal, blackened hook and low dorsomesal lobe with row of small spinose setae. Phallus with long, dorsal, rodlike sclerite, apicoventrally with recurved, ribbonlike sclerite, internally with plate bearing small teeth and c-shaped sclerite.

Female.—Length of forewing, 4 mm. Color light, golden-brown; hair on head and thorax mesally, white;

forewings light, golden-brown. Genitalia: Lobes of eighth sternum long and narrow, internally with linear, V-shaped sclerite extending length of segment with point at base of ninth segment. Ninth segment with darkened, V-shaped vaginal entrance basomesally on venter. Vaginal sclerite circular, with round, central opening placed mesally near base of eighth segment.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC.** **Pedernales Province:** Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al. (CMNH). Paratypes: Same data, 1♂ (NMNH). [**San Cristobal Province:** at or near Naranjo Dulce, 13 km N San Cristobal], S. Francisco Mts., Sept 1905, Aug. Busck, 1♀ (NMNH).

Genus *Polycentropus* Curtis

This genus is worldwide in distribution, and found in all regions of the New World. It is well represented on the Greater Antillean islands with four species described from Cuba, one each from Jamaica and Puerto Rico, and now five from Hispaniola. The abundant new material has permitted the certain association of males and females, thus adding females to some previously recorded species. The larvae are well known, with the Puerto Rican

P. zaneta (Flint, 1964) and the Jamaican *P. jamaicensis* (Flint, 1968a) described.

Polycentropus domingensis Banks

Polycentropus domingensis Banks, 1941:399, figs. 18, 19, 23 [♂]. Flint, 1967:6, fig. 21 [lectotype, ♂]; Flint, 1976:237, figs. 7–8 [♂]; Hamilton, 1988:175, fig. 7.18 [♂].

New material from the Central Cordillera has contained examples of this, the first described species of the genus from Hispaniola. The original types came from the Province of La Vega and we now add the Province of Peravia.

Material Examined.—DOMINICAN REPUBLIC. **Peravia Province:** upper Río Las Cuevas, 3 km SW La Nuez, 18°40'N, 70°36'W, 1880 m, 5–6 August 1990, Rawlins & Thompson, 10♂ (CMNH, NMNH); same, but 2 September 1995, Rawlins et al., 1♂, 1♀ (CMNH); same, but 5–6 October 1991, 9♂ (CMNH, NMNH). **La Vega Province:** Reserva Científica Valle Nuevo, Sector La Nevera, 3 km WNW La Nuez, 18°42'N, 70°36'W, 2200 m, 7 October 1992, Rawlins et al., 3♂ (CMNH, NMNH). Near Alto Bandera Pass, Res. Sta. Fund. Moscoso Puello, 2400 m, 8–9 May 2001, Woodruff & class, 1♂ (FSCA). Loma Rucilla, 8–10,000 ft [2440–3050 m], June '38 [1938], Darlington, ♂ lectotype, 2♂, 1♀ paratypes (MCZ). Valle Nuevo, SE Constanza, c. 7,000 ft. [2135 m], Aug. '38, Darl[ington], 6♂, 1♀ paratypes (MCZ).

Polycentropus jeldesi Flint

Polycentropus jeldesi Flint, 1976:237, figs. 9–10 [♂]. Hamilton, 1988:173, fig. 7.16 [♂].

Polycentropus species 2 Flint, 1976:239, fig. 19 [♀]. **New synonym.** *Polycentropus* “sp.A” Botosaneanu, 1996:15, figs.29–30 [♀]. **New synonym.**

This species has proven to be the most abundant in the new material here recorded. The associated females permit the firm placement of species 2 (Flint, 1976) and sp. A (Botosaneanu, 1996) as females of this species. It was originally described from La Vega Province; the new material extends its range into the Sierra de Neiba in the Province of Independencia and further along the Cordillera Central into Peravia and Elias Piña Provinces and to the border with the Province of Monseñor Nouel.

Material Examined.—Dominican Republic. **Elias Piña Province:** 4 km SE Río Limpio, ca. 760 m, 24–25 May 1973, D. & M. Davis, 1♀ (NMNH). **Independencia Province:** Sierra de Neiba near crest, 5.5 km NNW Angel Feliz, 18°41'N, 71°47'W, 1750 m, 21–22 July 1992, Rawlins et al., 11♂ (CMNH, NMNH); same but just south of crest, 5 km NNW Angel Feliz, 1780 m, 13–15 October 1991, 1♂ (CMNH). **La Vega Province:** Convento, 12 km S. of Constanza, 6–13 June 1969, Flint & Gómez, ♂ holotype, 6♀ (NMNH); same, but 18°51.5'N, 70°41.9'W, 1400 m, 6 May 1995, Flint, 1♀ (NMNH). 11.5 km S of Constanza (1 km N El Convento), 18°51.7'N, 70°41.0'W, 1410 m, 27 March 1999, Flint, 2♂, 40♀, many larvae, pupae, ♀ metamorphotypes (NMNH). Constanza, 8 November 1984, Spangler et al., 3♂ (NMNH). Cord. Central, Constanza-El Convento; Salto Agua Blanca, 11 May 1995, L. Botosaneanu, light, 3♀ (ZMUA). Cord. Central, Parque Nac. A. Bermudez, Arroyo M. Estrella, 25 April 1995, L. Botosaneanu, light, 1♀ (ZMUA). 2.5 km SW Piñar Bonito, 18°51'N, 70°43'W, 1430 m, 26 November 1992, Rawlins et al., 5♂, 13♀ (CMNH, NMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, R.E. Woodruff, 3♂, 9♀ (FSCA); same, but 20–21 April 2000, Woodruff & Henry, 1♂ (FSCA). **La Vega-Monseñor Nouel Provinces:** Loma el Casabito, summit, 19°03'N, 70°31'W, 1390 m, 19–23 November 1992, Rawlins et al., 83♂,

21♀ (CMNH, NMNH). **Monseñor Nouel Province** [not La Vega as labelled]: 6 km [not mi as labelled] NW of Rt.1 on road to Constanza, 27 June 1998, Woodruff & Baranowski, 4♀ (FSCA). 1 km E Paso alto de Casabito, 7 km NW la Ceiba, 19°02'N, 70°29'W, 1130 m, 28 July 1992, Rawlins et al., 3♂, 10♀ (CMNH). Paso alto de Casabito, 8 km NW la Ceiba, 19°02'N, 70°29'W, 1280 m, 28 July 1992, Rawlins et al., 3♂, 3♀ (CMNH). **Peravia Province:** upper Río Las Cuevas, 3 km SW La Nuez, 18°40'N, 70°36'W, 1880 m, 5–6 August 1990, Rawlins & Thompson, 17♂, 10♀ (CMNH, NMNH); same, but 2 September 1995, Rawlins et al., 1♂ (CMNH); same, but 5–6 October 1991, 13♂, 10♀ (CMNH, NMNH).

Polycentropus marcanoi Flint

Polycentropus marcanoi Flint, 1976:238, figs. 11, 12, 18 [♂, ♀]. Hamilton, 1988:171, fig. 7.14 [♂].

This is a rather widespread species on the lower hills and mountains. It was originally described from the Provinces of Dajabón, El Seibo, and Elias Piña. The provinces of La Vega and Puerto Plata are here added.

Material Examined.—DOMINICAN REPUBLIC. **Dajabón Province:** 9 km S Loma de Cabrera, 19°21'N, 71°37'W, 620 m, 12 July 1992, Rawlins et al., 1♂ (CMNH). **El Seibo Province:** Loma Cocuyo, 6 km N Pedro Sánchez, 18°55'N, 69°07'W, 475 m, 4 July 1992, Rawlins et al., 1♀ (CMNH). 7 mi [ca. 11 km] N Pedro Sánchez, Loma de Chivo, 5000 ft [1525 m], 20 June 1998, Woodruff & Freytag, 2♀ (FSCA). **La Vega Province:** 5 km SSE Jarabacoa, 640 m, 25 July 1987, Rawlins, 1♂ (CMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, R.E. Woodruff, 1♂, 2♀ (FSCA). **Monseñor Nouel Province** [not La Vega as labelled]: 6 km [not mi as labelled] NW of Rt.1 on road to Constanza, 27 June 1998, Woodruff & Baranowski, 2♂ (FSCA). **Puerto Plata Province:** Pico El Murazo, N slope near summit, 19°41'N, 70°57'W, 910 m, 28 November 1992, Rawlins et al., 4♂, 3♀ (CMNH, NMNH). **San Juan Province:** 7 km N Arroyo Caño, 1 km S Los Frios, 18°52'N, 71°01'W, 1120 m, 1 September 1995, Rawlins et al., 1♂ (CMNH).

Polycentropus pedernales Flint and Sykora, **new species** (Fig. 35)

Polycentropus “sp.B” Botosaneanu, 1996:15, figs. 31–34 [♀]. **New synonym.**

This, the smallest species yet taken on Hispaniola, seems limited to foothills and mountains of the Sierra de Baoruco. It seems to be the species ancestral to *P. marcanoi* in that the preanal appendage is elongate and bears specialized setae ventrally, and has the preanal and intermediate appendages approximate at the base. However *P. pedernales* lacks the small, mesal, spinose process from the inner face of the intermediate appendage seen in *P. marcanoi* and the vertical brace of the inferior appendage slopes evenly almost to the tip of the ventral lobe and it bears a spur at the junction with the ventral lobe.

Adult Male.—Length of forewing, 6.5–7 mm. Color dark brown, venter, legs, antennae stramineous; forewing brown with many spots of golden hair scattered overall, but largest on anterior wing margin. Genitalia: Ninth segment with slightly sinuate anterior margin. Tenth tergum lightly sclerotized ventrally, with elongate ventromesal lobe. Preanal appendage long, slender,

slightly arched; bearing on ventral and apicomeral surface short, specialized setae. Intermediate appendage lacking mesal process, with subapical excision bearing seta mesally. Inferior appendage with dorsal appendage long, curved ventrad apically; vertical brace long, tapering nearly to apex of ventral lobe, posterior tooth displaced to mesal face of ventral lobe; ventral lobe rounded apically, barely extending beyond posterior tooth. Phallus lightly sclerotized, with a small, curled sclerite internally.

Female.—Length of forewing, 7–8 mm. Color as in male. Genitalia: Lobes of eighth sternum small, nearly circular in outline. Ninth sternum trilobate, lateral lobes as long as broad, quadrate in outline, mesal lobe broad, posterior margin produced and angulate mesally. Vaginal sclerites consisting of posterolateral, pouchlike lobes and anteromesal rounded sclerite with rimmed central opening.

Type Material.—Holotype, male: **DOMINICAN REPUBLIC**. Pedernales Province: along Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, riparian woodland, J. Rawlins, S. Thompson, C. Young, R. Davidson (CMNH). Paratypes: Same data 8♂, 18♀ (CMNH, NMNH); same, but 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, O.S. Flint, 5♀ (NMNH, CMNH); same, but 18 March 1999, 2♂, 7♀, 1♂ metamorphotype (NMNH); same, but 20 March 1999, 16♀ (NMNH). Stream & falls, 19 km N Pedernales, 230 m, 18°09.2'N, 71°44.8'W, 19 March 1999, O.S. Flint, 7♀, 1♂ metamorphotype (NMNH). 23.5 km N Cabo Rojo, 18°06'N, 71°38'W, 540 m, 26–27 September 1991, wet deciduous forest, J. Rawlins, S. Thompson, C. Young, R. Davidson, 1♀ (CMNH). Sierra de Baoruco, Río Mulito 2 km from Mencia de Pedernales, 5 May 1995, L. Botosaneanu, light, 3♀ (ZMUA). **Barahona Province**: Limar Mine, nr. Filipinas, 26 June–7 July 1992, R. Woodruff & P. Skelley, 3♂, 1♀ (FSCA, NMNH). Sierra de Baoruco, Arroyo San Rafael, 4 May 1995, L. Botosaneanu, light, 1♀ (ZMUA).

Polycentropus vanderpooli Flint

Polycentropus vanderpooli Flint, 1976:237, figs. 5, 6 [♂]. Hamilton, 1988:176, fig. 7.19 [♂]; Botosaneanu, 1996:15, figs. 27, 28 [Dominican Republic, ♀].

Originally described from La Vega and Elias Piña provinces, it was later recorded from another locality in La Vega and its female also described (Botosaneanu, 1996). The new material extends its range greatly in the Provinces of Azua, Baoruco, Independencia, Pedernales, and the Distrito Nacional.

Material Examined.—**DOMINICAN REPUBLIC**. **Azua Province**: Río Las Cuevas, 8 km NE Padre Las Casas, 18°46'N, 70°53'W, 580 m, 3–4 October 1991, Rawlins et al., 2♀ (CMNH). **Baoruco Province**: Sierra de Neiba, Los Guineos on upper Río Colorado, 18°35'N, 71°11'W, 630 m, 11–12 August 1990, Rawlins & Thompson, 4♂, 3♀ (CMNH). [**Distrito Nacional**]: Cachón de la Rubia, nr. Central Ozama, 10 June 1969, Flint & Gómez, 1♀ (NMNH). **Elias Piña Province**: Río Limpio, 2400 ft [ca. 730 m], 26–27 April 2000, Woodruff & Henry, 3♂, 7♀ (FSCA). **Independencia Province**: Loma de Vientos, 4 km S Los Pinos, 18°35'N, 71°46'W, 475 m, 12 October 1991, Rawlins et al., 2♀ (CMNH); same, but 23 July 1992, 1♀ (CMNH). Río Guyabal, 4.5 km N Postrer Río, 150 m, 18°34.7'N, 71°37.7'W, 25 March 1999, Flint, 1♂, 2♀ (NMNH). **La Vega Province**: near mouth Arroyo Los Dajao, 5 km E Manabao, 19°04'N, 70°45'W, 740 m, 9 October 1991, Rawlins et al., 1♀ (CMNH). 5 km SSE Jarabacoa, 640 m, 25 July 1987, Rawlins, 2♂

(CMNH, NMNH). La Cienega de Manabao, Park Headquarters, 3–5 July 1999, Woodruff, 1♂ (FSCA). La Cienega, Río Yaque del Norte, 19°51.68'N, 70°51.68'W, 3640 ft. [ca. 1110 m], 29 July 1999, Peralta, 1♂, 1♀ (NMNH). **Pedernales Province**: 1 km S Los Arroyos, 18°14'N, 71°45'W, 1125 m, 18 October 1991, Rawlins et al., 1♂ (CMNH). Río Mulito, 21 km N Pedernales, 18°09.3'N, 71°45.4'W, 280 m, 6 May 1995, Flint, 1♀ (NMNH); same, but 18 March 1999, Flint, 3♂, 1♀ (NMNH); same, but 20 March 1999, 3♂, 7♀ (NMNH).

Family Xiphocentronidae Genus *Xiphocentron* Brauer

The genus *Xiphocentron* has been found from the southwestern United States, south to west central Argentina, including all the Greater and most of the Lesser Antilles. Most of the species are quite similar in appearance, especially those from the Greater Antilles, leading to a good deal of confusion in the taxonomic status of the various forms. The larvae, pupae, and tubular nets of *X. haitiense* from Puerto Rico were described by Flint (1964), and the larva and net of *X. messapus* from Texas by Wiggins (1996).

Xiphocentron (Antillotrichia) haitiense (Banks)

Antillotrichia haitiensis Banks, 1941:402, figs. 35, 36 [♂].

Xiphocentron haitiensis (Banks): Flint, 1964:26, figs. 5A–B, E, 6A–N [♂, ♀, larva, pupa, biology].

Xiphocentron (Antillotrichia) cubanum haitiense (Banks): Botosaneanu, 1996:12 [♂].

We have material in series from several sites in southeastern Dominican Republic which we have compared with the type and Puerto Rican examples of *X. haitiense* and Cuban examples of *X. cubanum*. There are several very clear and distinctive differences between the Cuban and Hispaniolan–Puerto Rican material that lead us to consider these to be distinct species. In *X. haitiensis* the anterior margin of the ninth sternum is truncate with perhaps a very small point from its ventral angle, in the *X. cubanum* the anterior margin tapers into a point that may be blunt or sharp. The posteroventral margin the ninth segment is distinctly emarginate mesally; in the *X. cubanum* this area is either nearly transverse with a pair of small, submesal angles or is produced. The anteromesal region of the tenth tergum is barely emarginate in *X. haitiensis*, but cleft for at least half its length in the Cuban. The ventral margin of the inferior appendage in lateral aspect is distinctly constricted near its base in *X. haitiense* but regularly tapering in *X. cubanum*. The type of *X. cubanum* (in which only the base of all the appendages is left) agrees in the shape of the anterior and posterior margins of the ninth sternum, anterior margin of the tenth tergum, and base of the inferior appendage.

The species is known from the type from Haiti, and recorded from Puerto Rico and Pedernales Province in the Dominican Republic. We here add the provinces of Barahona and Independencia.

Material Examined.—**DOMINICAN REPUBLIC.** **Barahona Province:** San Rafael, 8.3 km S Baoruco, 18°01.9'N, 71°08.4'W, 30 m, 15 May 1995, Flint, 10♀ (NMNH). **Independencia Province:** Río Las Damas, 2 km S Duvergé, 10 m, 18°22.0'N, 71°31.4'W, 24 March 1999, Flint & Mathis, 6♂, 1♀ (NMNH). La Descubierta, 0 m, 18°34.1'N, 71°43.8'W, 25 March 1999, Flint, 2♀ (NMNH). Río Guyabal, 4.5 km N Postrer Río, 150 m, 18°34.7'N, 71°37.7'W, 25 March 1999, Flint, 1♂, 1♀ (NMNH). **Pedernales Province:** along Río Mulito, 13 km N Pedernales, 18°09'N, 71°46'W, 230 m, 17 July 1992, Rawlins et al., 114♂, 16♀ (CMNH, FSCA); same, but 21 km N Pedernales, 18°09.3'N, 71°45.6'W, 280 m, 14 May 1995, Flint, 9♂ (NMNH); same, but 18 March 1999, Flint, 1♂, 1♀ (NMNH); same, but 20 March 1999, Mathis, 1♂ (NMNH). Sierra de Baoruco, Río Mulito, 2 km from Mencia de Pedernales, 5 May 1995, L. Botosaneanu, light, 1♂ (ZMUA).

HAITI. [Département du Sud]: Camp Perrin, nr 1000 ft [305 m], 8–27 Oct 1934, Darlington, ♂ holotype (MCZ).

PUERTO RICO. Dona Juana, Toro Negro Forest, 23–24 June 1969, Flint, 1♂, 6♀ (NMNH).

Xiphocentron species

Material of a second species from the Cordillera Central is available, but only in the female sex. It differs strongly in coloration from *X. haitiense*: the forewing is black with silver spots, one on the anterior margin, two on the posterior margin and small, silver dots along the apical margin. *Xiphocentron haitiense* is brown with irregular pale brown maculae. Considering the small differences in the male genitalia between species in this genus, we leave it undescribed for now.

Material Examined.—**DOMINICAN REPUBLIC, Monseñor Nouel Province:** near Jima [6.3 km W jct. Carretera Duarte and rt. 12], 19°01.2'N, 70°28.8'W, 670 m, 6 May 1995, Flint, 1♀ (NMNH). **La Vega Province:** near Agua Blanca, 13.7 km SE Constanza, 18°51.6'N, 70°41.9'W, 1505 m, 7 May 1995, Flint, 1♀ (NMNH).

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APPENDIX I

Checklist of the known Hispaniolan Trichoptera, with their known distributions

Family Calamoceratidae

1. *Phylloicus iridescens* Banks, Dominican Republic.
2. *Phylloicus pulchrus* Flint, Puerto Rico, Dominican Republic.

Family Ecnomidae

3. *Anstrobinodes labiatus* new species, Dominican Republic.

Family Glossosomatidae

4. *Caupsiophora pedophila* Flint, Puerto Rico, Dominican Republic, Haiti.

5. *Cariboptila aurulenta* Flint, Dominican Republic.
6. *Cariboptila caab* Botosaneanu, Dominican Republic.
7. *Cariboptila calcigena* Flint, Dominican Republic.
8. *Cariboptila hispaniolica* Flint, Dominican Republic.
9. *Cariboptila mathisi* new species, Dominican Republic.
10. *Cariboptila paradoxa* new species, Dominican Republic.

Family Helicopsychidae

11. *Helicopsyche (Feropsyche) altercoua* Botosaneanu and Flint, Dominican Republic.

12. *Helicopsyche* (*Feropsyche*) *dominicana* Botosaneanu and Flint, Dominican Republic.
13. *Helicopsyche* (*Feropsyche*) *parahageni* new species, Dominican Republic.
14. *Helicopsyche* (*Feropsyche*) *haitiensis* Banks, Haiti.
15. *Helicopsyche* (*Feropsyche*) *kalaom* Botosaneanu, Dominican Republic.
16. *Helicopsyche* (*Feropsyche*) *lutea* (Hagen), Dominican Republic.
17. *Helicopsyche* (*Feropsyche*) *nigrisensilla* Botosaneanu and Flint, Dominican Republic.
18. *Helicopsyche* (*Feropsyche*) *melanochaeta* new species, Dominican Republic.
19. *Helicopsyche* (*Feropsyche*) *poliochaeta* new species, Dominican Republic.
20. *Helicopsyche* (*Feropsyche*) *septifera* new species, Dominican Republic.

Family Hydrobiosidae

21. *Atopsyche* *batesi* Banks, Haiti.
22. *Atopsyche* *conventica* Flint, Dominican Republic.
23. *Atopsyche* *davisorum* Flint, Dominican Republic.
24. *Atopsyche* *hinulus* new species, Dominican Republic.
25. *Atopsyche* *lilicae* Botosaneanu, Haiti.
26. *Atopsyche* *orientalis* new species, Dominican Republic.
27. *Atopsyche* *peravia* new species, Dominican Republic.
28. *Atopsyche* *taina* Flint, Dominican Republic.
29. *Atopsyche* *thomasi* new species, Haiti.
30. *Atopsyche* species, ♀, Dominican Republic.
31. *Atopsyche* species, ♀, Haiti.

Family Hydropsychidae

32. *Calosopsyche* *batesi* (Flint), Haiti.
33. *Calosopsyche* *bohio* (Botosaneanu), Haiti.
34. *Calosopsyche* *carinifera* (Flint), Dominican Republic.
35. *Calosopsyche* *domingensis* (Banks), Dominican Republic.
36. *Macronema* species, larva, Haiti.
37. *Streptopsyche* *antilles* (Ross and Palmer), Dominican Republic, Haiti.
38. *Streptopsyche* *davisorum* Ross and Unzicker, Dominican Republic.
39. *Streptopsyche* *parander* (Botosaneanu), Dominican Republic.
40. *Streptopsyche* *rawlini* new species, Haiti.
41. *Streptopsyche* *praecipua* new species, Haiti.
42. *Smicridea* (*Smicridea*) *brunescens* new species, Dominican Republic.
43. *Smicridea* (*Smicridea*) *conma* Banks, Cuba, Dominican Republic.
44. *Smicridea* (*Smicridea*) *banksi* Flint, Haiti, Dominican Republic.
45. *Smicridea* (*Smicridea*) *completa* Banks, Dominican Republic.
46. *Smicridea* (*Smicridea*) *duarte* new species, Dominican Republic, Haiti.
47. *Smicridea* (*Smicridea*) species, ♀, Dominican Republic.

Family Hydroptilidae

48. *Alisotrichia* *aglae* Botosaneanu, Haiti, Dominican Republic.
49. *Alisotrichia* *aguaecadensis* Botosaneanu, Haiti, Dominican Republic.
50. *Alisotrichia* *arcana* Botosaneanu, Haiti.
51. *Alisotrichia* *bisetosa* new species, Dominican Republic.
52. *Alisotrichia* *euphrosyne* Botosaneanu, Haiti, Dominican Republic.
53. *Alisotrichia* *hirudopsis* *aitija* Botosaneanu, Dominican Republic.
54. *Alisotrichia* *hispaniolina* Botosaneanu, Haiti, Dominican Republic.
55. *Alisotrichia* *thalia* Botosaneanu, Haiti, Dominican Republic.
56. *Alisotrichia* *woodruffi* new species, Dominican Republic.
57. *Alisotrichia* *ultima* new species, Dominican Republic.
58. *Hydroptila* *ditalea* Flint, Jamaica, Dominican Republic, Mexico to Peru.
59. *Hydroptila* *dominicana* Botosaneanu, Dominican Republic, Cuba.
60. *Hydroptila* *medinai* Flint, Puerto Rico, Dominican Republic, Haiti, Cuba.

61. *Leucotrichia* *gomezi* Flint, Dominican Republic.
62. *Leucotrichia* *tubifex* Flint, Puerto Rico, Dominican Republic, Haiti, Jamaica.
63. *Metrichia* *cafetalera* Botosaneanu, Cuba, Dominican Republic.
64. *Metrichia* *fontismoreaui* (Botosaneanu), Haiti, Dominican Republic.
65. *Metrichia* *kunanskii* (Botosaneanu), Haiti, Dominican Republic.
66. *Metrichia* *longispina* new species, Dominican Republic.
67. *Metrichia* *squamigera* Flint, Puerto Rico, Dominican Republic.
68. *Metrichia* species, ♀, Haiti.
69. *Neotrichia* *iridescent* Flint, Puerto Rico, Dominican Republic, Cuba, Jamaica, Guadeloupe to St. Lucia.
70. *Neotrichia* *bifurcata* Harris, new species, Dominican Republic.
71. *Neotrichia* *pequenita* Botosaneanu, Cuba, Dominican Republic, Haiti, Jamaica, Barbados, Trinidad.
72. *Neotrichia* species, ♀, Haiti.
73. *Ochrotrichia* *baorucoensis* new species, Dominican Republic.
74. *Ochrotrichia* *cachonera* Botosaneanu, Dominican Republic.
75. *Ochrotrichia* *ingloria* Botosaneanu, Dominican Republic.
76. *Ochrotrichia* *larimar* new species, Dominican Republic.
77. *Ochrotrichia* *obovata* new species, Dominican Republic.
78. *Ochrotrichia* *seiba* new species, Dominican Republic.
79. *Ochrotrichia* *serra* Botosaneanu, Haiti.
80. *Ochrotrichia* *verda* Flint, Puerto Rico, Dominican Republic.
81. *Ochrotrichia* species A, ♀, Dominican Republic.
82. *Ochrotrichia* species B, ♀, Dominican Republic.
83. *Orthotrichia* *aegerfasciella* (Chambers), USA, Dominican Republic, Cuba, Haiti, Canada to Panama.
84. *Orthotrichia* *cristata* Morton, USA, Dominican Republic, Cuba, Jamaica, Canada to Florida and Texas.
85. *Oxyethira* (*Mesotrichia*) *albaequae* Botosaneanu, Dominican Republic.
86. *Oxyethira* (*Dampftrichia*) *nirebalina* Botosaneanu, Haiti, Dominican Republic.
87. *Oxyethira* (*Mesotrichia*) *geminata* new species, Dominican Republic, Haiti.
88. *Oxyethira* (*Mesotrichia*) *ortizorum* Botosaneanu, Dominican Republic.
89. *Oxyethira* (*Mesotrichia*) *scopulina* new species, Dominican Republic.
90. *Oxyethira* (*Dampftrichia*) *cirrifera* Flint, Puerto Rico, Dominican Republic, Cuba, Haiti, Jamaica, Dominica, Martinique.
91. *Oxyethira* (*Loxotrichia*) *janelle* Denning, USA, Dominican Republic, Cuba, Haiti, Jamaica, Puerto Rico, Guadeloupe, Dominica, southern USA to Costa Rica.
92. *Oxyethira* (*Loxotrichia*) *puertoricensis* Flint, Puerto Rico, Dominican Republic, Cuba, Haiti, Jamaica.
93. *Oxyethira* (*Dampftrichia*) *sinulatrix* Flint, Jamaica, Dominican Republic, Cuba, Haiti, Mexico to Panama.
94. *Oxyethira* (*Dampftrichia*) *tega* Flint, Jamaica, Dominican Republic, Cuba, Haiti, Jamaica, Guadeloupe, Dominica.
95. *Oxyethira* (*Mesotrichia*) species, ♀, Dominican Republic.

Family Leptoceridae

96. *Nectopsyche* *cubana* (Banks), Cuba, Dominican Republic, Haiti, Jamaica, Puerto Rico.
97. *Oecetis* *inconspicua* (Walker), USA, Dominican Republic, Cuba, Haiti, Jamaica, Puerto Rico, Trinidad, Canada to north South America.
98. *Oecetis* *haitises* new species, Dominican Republic.
99. *Setodes* *anomalous* new species, Dominican Republic.

Family Odontoceridae

100. *Mariha* *gracilis* Banks, Haiti.
101. *Mariha* *nigrescens* Banks, Dominican Republic.
102. *Mariha* *valga* new species, Dominican Republic.

Family Philopotamidae

103. *Chimarra* (*Curgia*) *braconoides* (Walker), Dominican Republic, Haiti.

- 104. *Chimarra (Curgia) gilvamacula* Flint, Dominican Republic, Haiti.
- 105. *Chimarra (Chimarrita) merengue* Blahnik, Dominican Republic.
- 106. *Chimarra (Otarra) koki* Botosaneanu, Dominican Republic.
- 107. *Chimarra (Otarra) redonda* Blahnik, Dominican Republic.
- 108. *Chimarra (Otarra) spinulifera spinulifera* Flint, Haiti.
- 109. *Chimarra (Otarra) spinulifera galalcha* Botosaneanu, Dominican Republic.
- 110. *Chimarra (Otarra) spinulifera baornco* new species, Dominican Republic.

Family Polycentropodidae

- 111. *Antillopsyche denma* Botosaneanu, Dominican Republic.

- 112. *Cernotina daniehi* new species, Dominican Republic.
- 113. *Polycentropus domingensis* Banks, Dominican Republic.
- 114. *Polycentropus jekdesi* Flint, Dominican Republic.
- 115. *Polycentropus marcanoi* Flint, Dominican Republic.
- 116. *Polycentropus pedernales* new species, Dominican Republic.
- 117. *Polycentropus vanderpooli* Flint, Dominican Republic.

Family Xiphocentronidae

- 118. *Xiphocentron (Antillotrichia) haitiense* (Banks), Haiti, Dominican Republic, Puerto Rico.
- 119. *Xiphocentron (Antillotrichia)* species, ♀, Dominican Republic.

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BEAVERS (RODENTIA, CASTORIDAE) FROM THE RUNNINGWATER FORMATION
(EARLY MIOCENE, EARLY HEMINGFORDIAN) OF WESTERN NEBRASKAWILLIAM W. KORTH¹

Research Associate, Section of Vertebrate Paleontology

ABSTRACT

New material of fossil beavers from the early Hemingfordian (early Miocene) of western Nebraska represents five species, including one new genus (*Miotheriomys*), three new species (*Miotheriomys stenodon*, *Anchitheriomys nanus*, *Monosaulax baileyi*) and an indeterminate anchitheriomyine. Additional specimens of *Euroxenomys wilsoni*, previously known only from the Hemingfordian of Colorado, are also described. The earliest definite occurrence of *Monosaulax* is recognized from the Hemingfordian. The greatest diversity of the species recognized is in the Anchitheriomyinae (which is elevated to the rank of subfamily), being represented by five species from the Hemingfordian of North America.

KEY WORDS: Hemingfordian, Miocene, Castoridae, Anchitheriomyinae, Castoroidinae

INTRODUCTION

The Arikareean record of beavers from the northern Great Plains is dominated by the fossorially adapted Palaeocastorinae, represented by at least 14 species (Macdonald, 1963; Martin, 1987; Xu, 1996). Only one other species of beaver is known from this time, the agnotocastorine *Neotocastor hesperus* from Montana (Douglass, 1901; Korth, 1996). The Hemingfordian record of beavers from the Great Plains is much less diverse, being limited to only four species, *Anchitheriomys senrudi* (Wood, 1945; Korth, 2001a), *A. stouti* (Korth, 2001a), a possible species of *Hystriopsis* (referred to *Anchitheriomys* by Wilson, 1960; see Korth, 1998), and the castoroidine *Euroxenomys* (Wilson, 1960; Sutton and Korth, 1995; Korth, 2001b). In recent years, the University of Nebraska State Museum and the Nebraska State Department of Roads Highway Salvage Paleontol-

ogy program have undertaken extensive collection of vertebrate fossils in the Arikareean and Hemingfordian horizons of western Nebraska. The species described below were collected during these recent efforts, but also include several specimens that were collected by the University of Nebraska State Museum as early as the 1930s but were never published. The additional species of Hemingfordian beavers described below doubles the previously known record from that time.

Dental terminology follows that of Wood and Wilson (1936) along with special nomenclature for castorids presented by Stirton (1935). Abbreviations for institutions: UNSM, University of Nebraska State Museum. Precise locality data for fossil quarries listed as UNSM locality numbers are available in the records of that institution.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Castoridae Hemprich, 1820

Subfamily Anchitheriomyinae Korth, 2001a (new rank)

Anchitheriomys Roger, 1898

Anchitheriomys nanus, new species

(Fig. 1C-E; Table 1)

Type Specimen.—UNSM 26713, left P₄.

Referred Specimens.—UNSM 26714, 26715, 119814, isolated P₄s; UNSM 119815, M₃; and UNSM 26702 right P₄.

Horizon and Locality.—UNSM locality Bx-7 (Hemingford Quarry), Runningwater Formation, Box Butte County, Nebraska.

Diagnosis.—Smallest species of the genus; premolars shortened (anteroposteriorly) relative to width compared to other species.

Etymology.—Greek, *nanos*, dwarf.

Description.—The lower premolars are mesodont with two strong roots. The anterior width of the tooth is less than the posterior width. All of the teeth are nearly as wide (posteriorly) as they are long (Table 1). All of the P₄s have the simple, primitive occlusal pattern of castorids: a buccal hypoflexid and three lingual fossettids, para-, meso-, and metafossettids. However, the walls of all the fossettids are irregular and not smooth, and there is at least one small accessory fossettids on each of the specimens except on the tooth with the greatest amount of wear (UNSM 119814:Fig. 1D).

The holotype is the least worn and has the greatest number of irregularities (Fig. 1C). The mesoflexid (not yet closed lingually) is the

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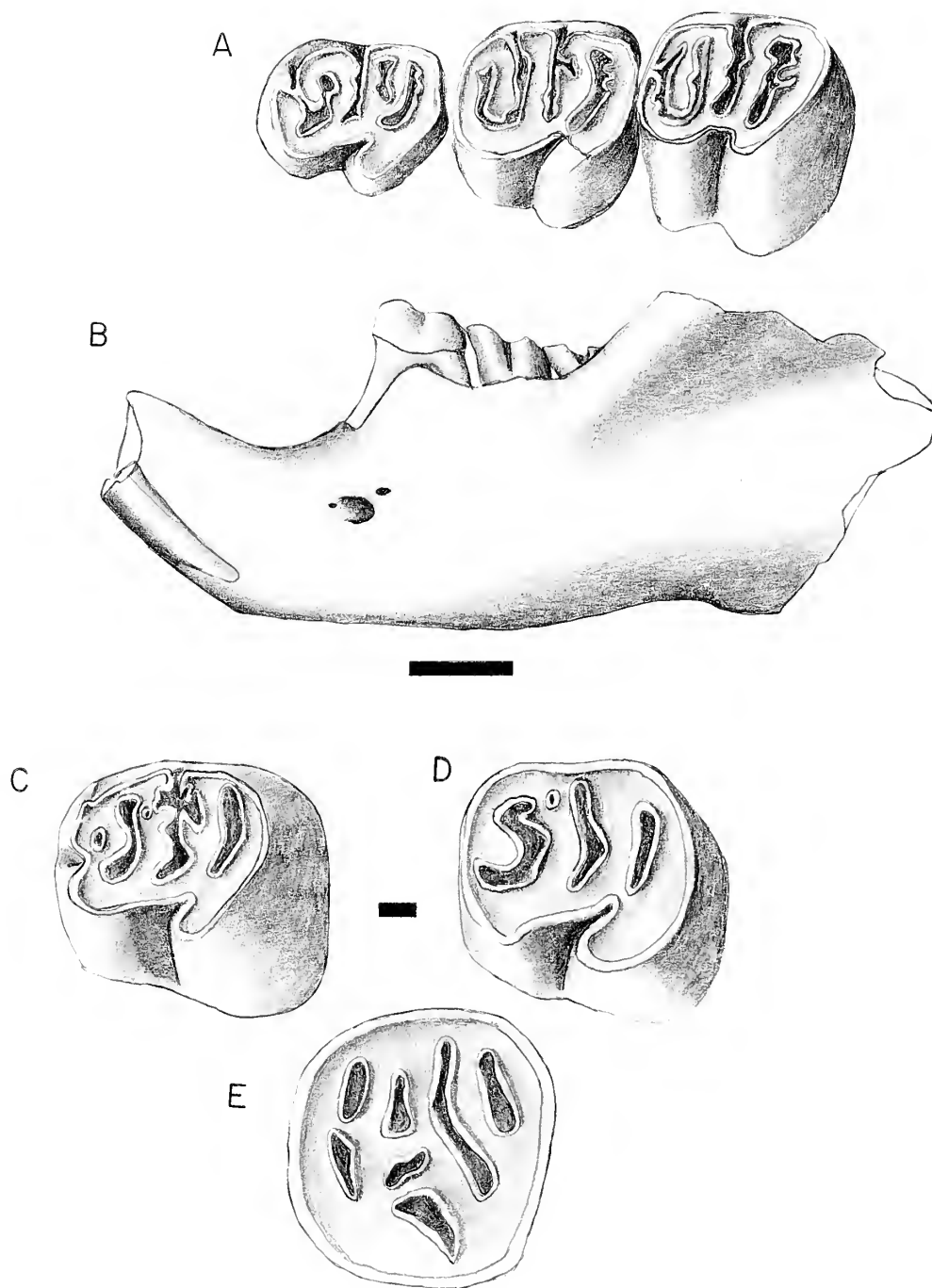


Fig. 1.—Dentition and mandibles of *Miotheriomys stenodon* and *Anchitheriomys nanus*. A, B. *M. stenodon*, holotype, UNSM 93064. A. Left dP₄–M₂. B. Lateral view of mandible. C–E. *A. nanus*. C. Holotype, UNSM 26713, left P₄. D. UNSM 26715, left P₄. E. UNSM 26702, left P₄. Bar scale for teeth = 1 mm. Bar scale for jaw = 5 mm.

most irregular with a wide (anteroposterior) expansion near its lingual end and an anteriorly directed spur near its center. Anterior to the parafofsettid is a small, circular accessory fofsettid and a narrow valley that breaks the anterior border of the occlusal surface near the buccal end of the parafofsettid. A minute accessory fofsettid is between the lingual ends of the mesofofsettid and the parafofsettid. A transversely elongated but small fofsettid is confluent with the lingual half of the mesofofsettid. Two specimens are moderately worn and possess only a single, small

accessory fofsettid. On both UNSM 26714 (Fig. 1D) and UNSM 26715 this accessory fofsettid is between the mesofofsettid and the parafofsettid near their lingual ends. The parafofsettid on UNSM 26715 bends posteriorly giving the fofsettid an S-shape.

The referred M₃, UNSM 119815, is three-rooted (two anterior, one posterior). It has the three major fofsettids (para-, meso-, metafofsettid) and two minute, circular accessory fofsettids; one anterior to the parafofsettid, the second between the mesofofsettid and metafofsettid.

The buccal end of the parafoissetid curves anteriorly, forming a J-shape. The mesofossetid is oriented buccolingually. The metafoissetid is gently convex posteriorly.

An isolated P⁴, UNSM 26702, from UNSM locality Bx-7 is assigned to *A. nanus* based on size (largest castorid from the Hemingford Quarry), crown height, and complexity of the fossettes comparable to those of the lower premolars of *A. nanus*. The P⁴ is more worn than the known lower premolars (Fig. 1E). It is shorter (anteroposteriorly) than wide. There are six transversely elongated fossettes on the occlusal surface. The anterior parafoissete, the lingual hypofossette, the metafoissete and an accessory fossette posterior to the metafoissetid are all oriented nearly parallel to one another in an anterobuccal to posterolingual direction. The parafoissete and metafoissete are slightly convex anteriorly. The mesofossette parallels the parafoissete and metafoissete but is very short, extending less than half of the width of the occlusal surface of the tooth. A small accessory fossette separates the lingual end of the mesofossette from the buccal end of the hypofossette. This accessory fossette is oriented perpendicular to the rest of the fossettes.

Discussion.—*Anchitheriomys nanus* is the smallest species of this genus ever reported, being just slightly smaller than *A. senrudi* (Wood, 1945) and much smaller than *A. stouiti* (Korth, 2001a) or the Barstovian or Eurasian species of the genus (Stirton, 1934, 1935; Voorhies, 1990a; Korth and Emry, 1997). The length of the largest specimen of *A. nanus* (UNSM 26714) is 18% smaller than that of the holotype of *A. stouiti* and 8% smaller than the holotype of *A. senrudi*. The mean of the lengths of the known P₄s of *A. nanus* (0.89) is 23% and 13% smaller than the respective holotypes of the former species. The proportions of the lower premolars (shorter relative to width) of *A. nanus* is different than in the other Hemingfordian species of the genus, *A. senrudi* and *A. stouiti*. The ratio of the width to length of P₄ in *A. nanus* ranges from 0.85 to 0.96, with a mean of 0.89. In *A. senrudi* this ratio is 0.84, and in *A. stouiti* it is 0.76. The later Miocene species such as *A. fluminis* have proportions similar to that of *A. nanus* (0.94; taken from figure of holotype [Stirton, 1935:fig 47]. The degree of complexity of the fossettes (-ids) on the cheek teeth of *A. nanus* is comparable to that of other species.

The recognition of *Anchitheriomys nanus* increases the number of Hemingfordian species of this genus to three. There is a single species from North America in the Barstovian and none known from the Arikarean, demonstrating the increase of *Anchitheriomys* species in the Hemingfordian after its immigration from Eurasia (Korth, 1998; 2001b), and equally dramatic reduction in the Barstovian.

Miotheriomys, new genus

Type Species.—*Miotheriomys stenodon* new species.

Range.—Early Hemingfordian (early Miocene) of Nebraska.

Etymology.—Miocene (intended to show age); *theros*, beast; *mys*, mouse.

Diagnosis.—Larger than *Propalaeocastor* and *Oligotheriomys*, smaller than *Anchitheriomys*; cheek teeth mesodont; upper cheek teeth strongly unilaterally hyp-

Table 1.—Dental measurements of *Anchitheriomys nanus*. Abbreviations: a-p, anteroposterior length; tr, transverse width; tra, anterior transverse width; trp, posterior transverse width. Measurements in mm.

UNSM#:	26713	26714	26715	119814	119815
P ₄ a-p	7.20	7.60	7.00	6.81	
P ₄ tra	5.85	5.60	5.20	5.03	
P ₄ trp	6.50	7.30	5.95	5.78	
M ₃ a-p					5.61
M ₃ tr					4.89
UNSM#:	26702				
P ⁴ a-p	6.90				
P ⁴ tr	7.60				

sodont (lingual crown height greater than buccal crown height); occlusal pattern of cheek teeth lack accessory fossettes (-ids) as in *Anchitheriomys* but with accessory crenulations on the lophs; lower cheek teeth with accessory lophid anterior to metalophid originating lingually, forming a U-shaped parafoissetid; P₄ slightly larger than the molars; protoloph on upper molars doubled, forming small loop; anteroposterior lophule divides metafoissete of upper molars into two; lower incisor narrow.

Discussion.—*Miotheriomys* is referable to the anchitheriomysines because of: 1) irregularities of the enamel on the fossettids of the cheek teeth; 2) long diastema; 3) cheek teeth rooted; and 4) weak development of the digastric process. It differs from *Oligotheriomys* in being larger with higher crowned cheek teeth, having P₄ larger than the molars. *Miotheriomys* differs from *Anchitheriomys* and *Propalaeocastor* in lacking a ridged incisor.

Miotheriomys stenodon, new species (Fig. 1A, B and 2; Table 2)

Type Specimen.—UNSM 93064, left mandible with incisor and dP₄–M₂.

Referred Specimens.—UNSM 119822, 119823, P⁴; UNSM 119824 to 119829, M¹ or M²; UNSM 119830 to 119833, M³; UNSM 26712, 119834, dP₄; UNSM 119835, 119836, P₄; UNSM 119837 to 119839, M₁ or M₂; UNSM 119840, M₃.

Horizon and Locality.—Type and all referred specimens from UNSM locality, BX-7, Runningwater Formation, Box Butte County, Nebraska.

Age.—Early Hemingfordian (early Miocene).

Diagnosis.—Only species of the genus.

Etymology.—Greek; *steno*, thin; *odon*, tooth.

Description.—The mandible is typically robust (Fig. 1B), as in all other castorids, but the digastric process and masseteric scar are poorly developed. The diastema is relatively long (13 mm) compared to the length of the tooth row. The mental foramen is below the anterior root of dP₄ at mid-depth of the mandible and there is a minute accessory foramen just dorsal and posterior to the mental foramen. Although the angle, coronoid process, and mandibular condyle are missing on the specimen, it is evident from posterior view that the horizontal ramus is

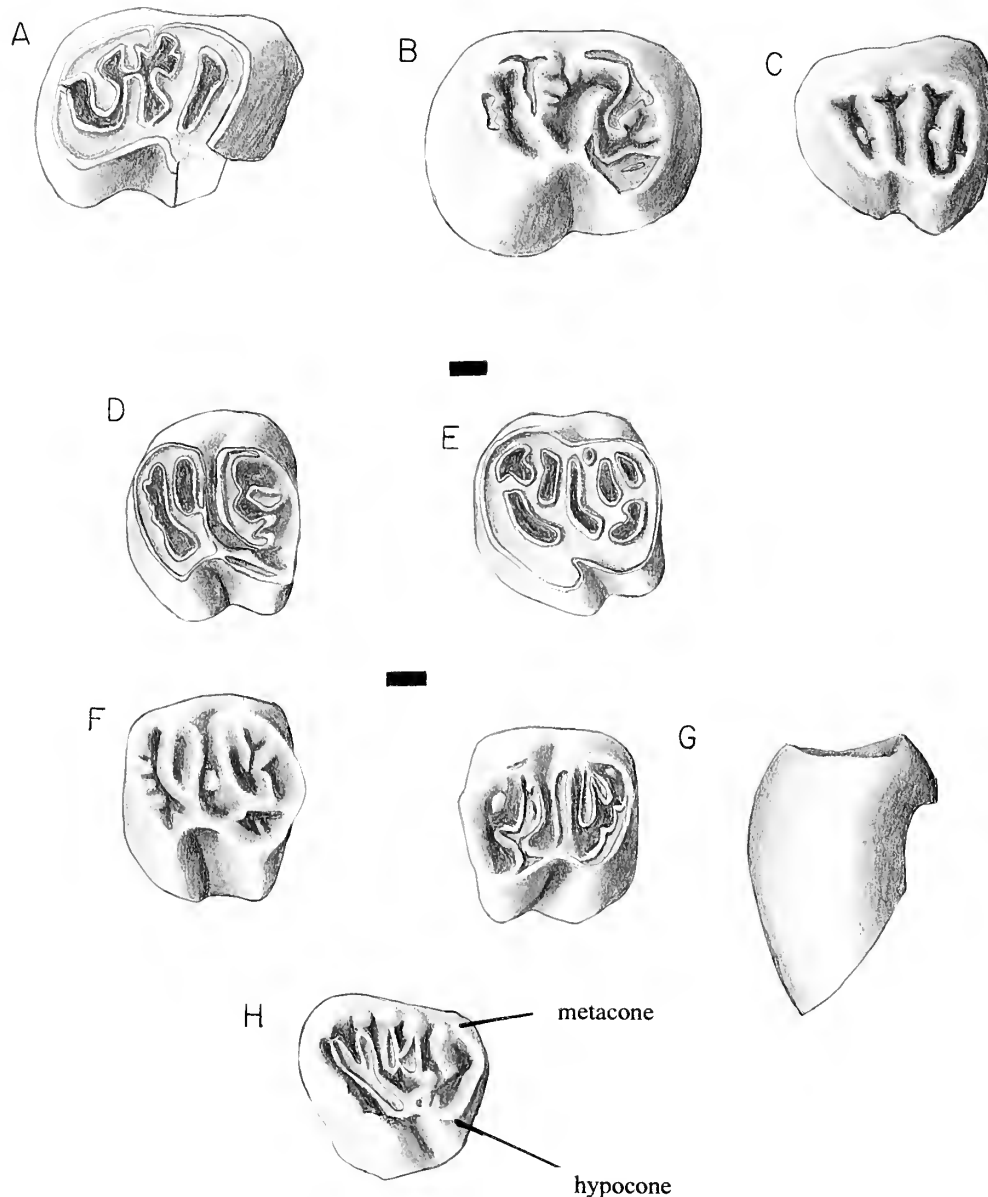


Fig. 2.—Cheek teeth of *Miotheriomys stenodon*. A. UNSM 119835, left P_4 . B. UNSM 119836, right P_4 . C. UNSM 119840, right M_3 . D. UNSM 119823, left P_4 . E. UNSM 119822, left P_4 . F. UNSM 119827, left M^1 or M^2 . G. UNSM 119824, right M^1 or M^2 (occlusal view left, anterior view right). H. UNSM 119831, left M^3 . Bar scale = 1 mm.

expanded ventrolaterally and would produce the zig-zag arrangement of the angle present in *Anchitheriomys* (Korth, 2001a, 2001c).

The lower incisor is rounded anteriorly with a faint groove down the center near its anterior end. The incisor is exposed below the cheek teeth and the groove is not present at this level, suggesting that it does not run the entire length of the tooth and may be a juvenile character. The lower incisor is not as wide (buccolingually) relative to the anteroposterior measurement of its cross section as in other castorids (Table 2).

The deciduous lower premolar (Fig. 1A) is the smallest of the teeth present. It is clearly deciduous because of its much lower crown height and widely splayed roots. The occlusal morphology is the typical pattern for primitive castorids. There is only a shallow hypoflexid on the buccal side of the tooth. The mesoflexid is still open lingually, extends nearly the entire width of the tooth, and is gently concave anteriorly. Anterior to the mesoflexid is a small parafoesettid that is nearly parallel to the

mesoflexid, but is narrowest in the center (pinched). There is a minute anterior arm of the parafoesettid that corresponds to a notch on the anterior margin of the tooth. On the posterior half of the tooth are two transversely elongated foesettds that also parallel the mesoflexid. The most posterior (metafoesettid) is the longest of the foesettds, nearly reaching the lingual end of the hypoflexid. Anterior to it is a much shorter foesettid that is only on the lingual half of the tooth. All of the flexids and foesettds have irregular sides.

Isolated lower premolars and M_3 s were assigned to this species because of comparable size with the holotype, comparable irregularities of the occlusal enamel, and the presence of the characteristic U-shaped parafoesettid. P_4 is larger than the molars. It is mesodont, slightly lower crowned than any species of *Monosaulax*. The crown is slightly higher buccally than lingually. The anterior width is less than the posterior width. There are numerous wrinkles and irregularities on all of the

lophids. The parafoissettid is U-shaped, formed by a short lophid running from the metaconid but not reaching the protoconid. The posterior arm of the protoconid extends lingually. On the worn specimen (UNSM 119835, Fig. 2A) it reaches the lingual edge of the tooth, whereas on the unworn specimen (UNSM 119836, Fig. 2B) it does not, leaving a narrow valley separating its lingual end from the side of the tooth. The mesoflexid is very complex with numerous irregularities, but generally extends directly buccally across the tooth. It closes off early in wear to form a mesofossettid. The hypolophid is complete from the entoconid to the hypoconid, producing an elongated, thin metafoissettid. The hypoflexid is shallow and directed posterolingually.

The first two lower molars (Fig. 1B) are smaller than P_4 and equal in size to one another. All of the flexids and fossettid on the molars have a great number of irregularities as in P_4 . The anterior width of the molars is subequal to the posterior width, unlike P_4 . The hypoflexid is very short and open buccally. The mesoflexid is also open on all referred molars. The mesostriid on the unworn molars extends about one-third to one-half the height of the crown, indicating that it will eventually close off lingually in more advanced stages of wear. The mesoflexid is similar to that of P_4 in length and appearance. The parafoissettid is U-shaped as in P_4 , being formed by a similar lophid. The base of the "U" (buccal end of the parafoissettid) appears very deep on all the known molars and will not isolate the parafoissettid into two parts until extremely late stages of wear. The posterior arm of the protoconid is complete to the lingual side of the tooth on all specimens. Only one fossettid is posterior to the mesoflexid, the metafoissettid. It is long, running nearly the entire width of the tooth, and gently concave anteriorly.

The third lower molar is the smallest (Fig. 2C). The anterior half is nearly identical to that of M_1 and M_2 . The posterior half tapers posteriorly, giving the tooth a triangular outline. There is no mesostriid, indicating that the mesofossettid is closed-off entirely even at the earliest stages of wear. The metafoissettid is straight and oriented obliquely, anterobuccally to posterolingually.

All upper cheek teeth are isolated specimens (Fig. 2D–G). They have been assigned to this species because of comparable size with the lower dental elements and because the nature and degree of irregularities on the occlusal surface agree with those of the lower cheek teeth. There is marked unilateral hypsodonty on all upper cheek teeth, the lingual height of the crown being between two and four times greater than the buccal height (Fig. 2G). Only two specimens have been identified as P^4 . They are distinguished from the referred upper molars by their slightly larger size and in having a convex anterior surface. The anterior and posterior walls of the referred molars are concave, whereas only the posterior wall of the premolars is. There is no indication of a wear facet on either of the P^4 s for a P^3 . As in the lower cheek teeth, the lophs have a number of complications and irregularities. The hypoflexus is shallow and directed anterobuccally. The parafoissette is convex anteriorly and runs the entire width of the tooth. On one specimen (UNSM 119822, Fig. 2E) it is separated into two smaller fossettes. The mesofossette is transversely elongated and bends posteriorly at its lingual end forming a J-shape. The protoloph is doubled. Two lophs originate at the paracone and run directly lingually, then fuse on the lingual half of the tooth and curve posteriorly to join the hypocone. The doubled protoloph forms a distinctive buccolingually elongated fossette between the parafoissette and the mesofossette that is preserved on even the most worn specimens. Posterior to the mesofossette are four smaller fossettes formed by the irregularities of the metaloph. The pattern of these smaller fossettes is different on each of the known P^4 s.

The anterior molars are nearly identical to P^4 . The parafoissette, mesofossette, and doubled protoloph are arranged as in P^4 . A distinct spur extends posteriorly from near the lingual end of the metaloph and separates a small lingual fossette. Buccal to this spur of the metaloph are several smaller fossettes that are irregular in shape and vary between different specimens. On one specimen (UNSM 119824, Fig. 2G) the doubled protoloph does not fuse its two parts at the lingual end.

M^3 is the smallest of the molars. The anterior half of the tooth is similar in morphology to the anterior molars. The parafoissette is straighter and the protoloph and mesofossette do not curve as strongly

Table 2.—Dental measurements of *Miotheriomys stenodon*. Abbreviations as in Table 1. Statistical abbreviations: N, number of specimens; M, mean; OR, range of variation; S, standard deviation; CV, coefficient of variation. All measurements represent maximum dimensions. * M^1 and * M_1 , measurements based on isolated teeth that may be either the first or second molars. P_4 – M_3 measurements taken at alveolar margin. Measurements in mm.

	N	M	OR	S	CV	type (UNSM 93064)
DP ₄ a–p	2	4.68	4.40–4.96			4.40
tr	2	3.47	3.45–3.48			3.45
P ₄ a–p	1	7.22				
tra	2	4.71	4.53–4.88			
trp	1	5.68				
* M_1 a–p	5	4.63	4.38–4.88	0.20	4.27	4.75
tr	5	5.03	4.79–5.49	0.29	5.72	4.80
M ₂ a–p						4.50
tr						5.10
M ₃ a–p	1	5.13				
tr	1	4.90				
I ₁ a–p						4.40
I ₁ tr						3.15
dP ₄ –M ₃						21.45
P ⁴ a–p	2	4.65	4.49–4.80			
tr	2	5.10	5.02–5.18			
* M^1 a–p	6	4.36	4.11–4.50	0.15	3.40	
tr	6	4.67	4.48–5.01	0.22	4.69	
M ₃ a–p	4	4.18	4.05–4.29	0.10	2.43	
tr	4	4.55	4.27–4.85	0.26	4.55	

posteriorly. The posterior half of the tooth is reduced and the tooth is triangular in shape. The metacone and hypocone are small, marginal cusps. Several small, isolated fossettes are formed from the irregularities of the posterior half of the occlusal surface.

Discussion.—*Miotheriomys* differs from *Anchitheriomys* by its smaller size and lack of a ridged incisor. The cheek teeth of *Miotheriomys* are more similar to those of *Oligotheriomys* than to those of any other beaver. The only other castorid with the unique loph on the lower cheek teeth that forms the U-shaped parafoissettid is *Oligotheriomys magnus* (see Wood, 1937:fig. 45; Korth, 2000a:fig. 2). The double protoloph and posterior spur of the metaloph of the upper molars of *Miotheriomys* are also present in *O. primus* (Korth, 1998:fig. 1). The unilateral hypsodonty of the upper molars of *Miotheriomys* is more greatly exaggerated than in any other known beaver, but is closer to that in *O. primus* than to other anchitheriomyines. This suggests that *Miotheriomys* is more closely related to *Oligotheriomys* than to *Anchitheriomys* and may have been directly derived from the earlier North American genus.

Anchitheriomyinae, genus and species indeterminate (Fig. 3)

Referred Specimen.—UNSM 26598, left mandible with P_4 and incisor.

Horizon and Locality.—UNSM locality Cr-128, Runningwater Formation, Cherry County, Nebraska.

Age.—Early Hemingfordian (early Miocene).

Measurements.— P_4 ; a–p = 5.77 mm; tra = 4.30 mm; trp = 5.00 mm; P_4 – M_3 (alveolar length) = 17.82 mm (see Table 1 for abbreviations).

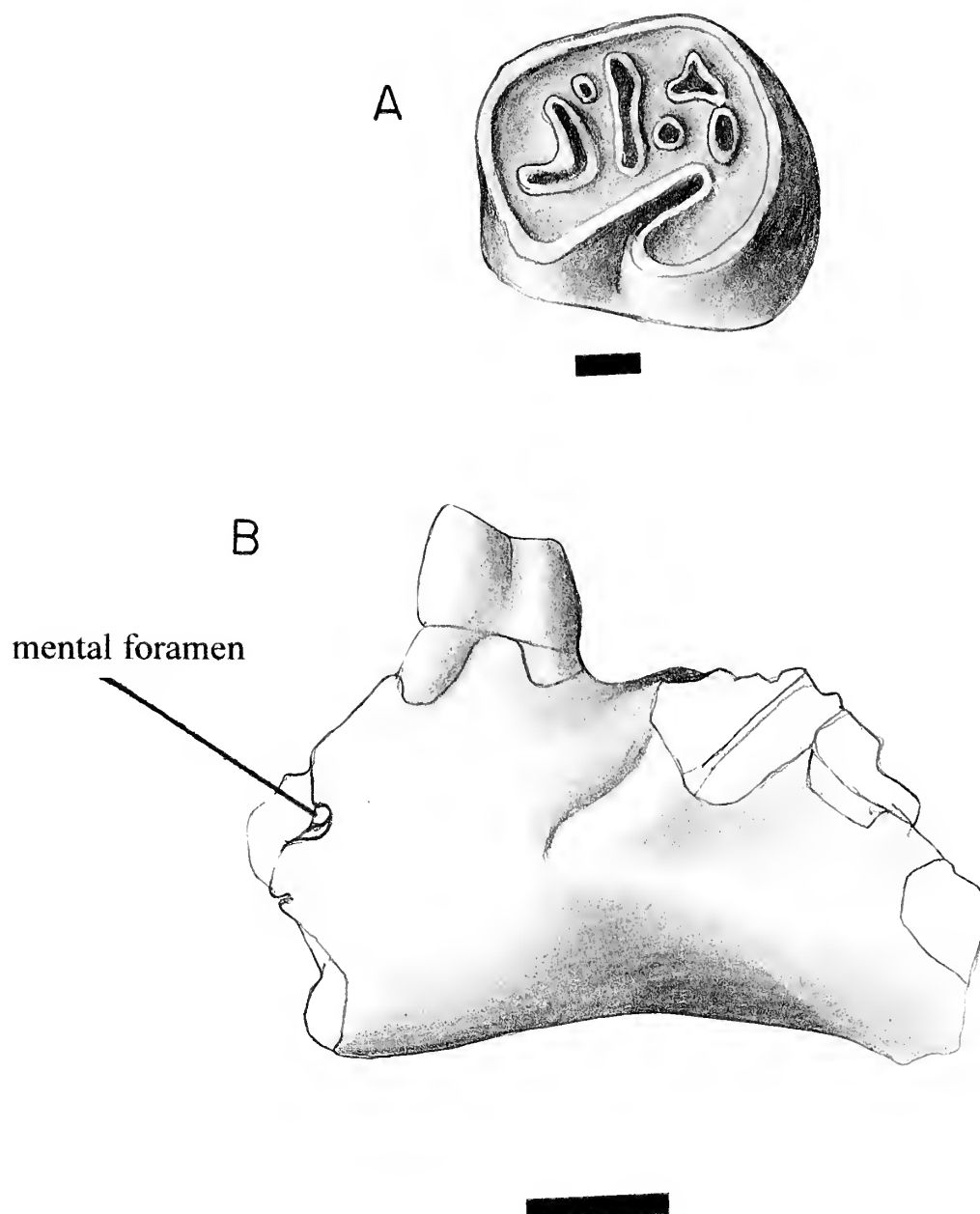


Fig. 3.—Anchitheromyine, genus and species indeterminate, UNSM 26598. A. Left P_4 . B. Lateral view of mandible. Bar scale for teeth = 1 mm. Bar scale for jaw = 5 mm.

Description.—In size, this species is similar to that of the Orellan *Oligotheriomys primus* but clearly smaller than any other North American species of *Anchitheriomys*, including *A. namus* (Table 1). The mandible is robust, but the diastema and ascending ramus are broken away. The mental foramen is relatively high on the side of the mandible, ventral to the anterior margin of P_4 , but only about one-third of the depth of the jaw from the margin of the diastema, and apparently doubled. The ascending ramus and angle of the mandible are missing; however, it is apparent that the anterior margin of the ascending ramus is farther forward than in other anchitheromyines. In others the ascending ramus rises above the alveolar margin even with the center or posterior margin of the second molar. In UNSM 26598, it originates anterior to the second molar.

The incisor is preserved only as several small chips of enamel that were within the alveolus. Although the entire cross section of the tooth was not preserved, several of the enamel pieces from the incisor that were extracted from the mandible preserve the entire anterior enamel surface. From these fragments it is evident that the incisor has a smooth, convex anterior surface. Based on the alveolus for the incisor, it is nearly as wide as long (anteroposteriorly) in cross section. P_4 is mesodont and rooted. The occlusal morphology is similar to that of other anchitheromyines, and more complex than other castorids. Lingually there is a posterolingually directed hypoflexid. Since the hypostridium extends to nearly the base of the crown, the hypoflexid should remain open buccally until the very latest stages of wear. There are no lingually open flexids on the tooth. The parafoissettid is V-shaped with the apex pointed

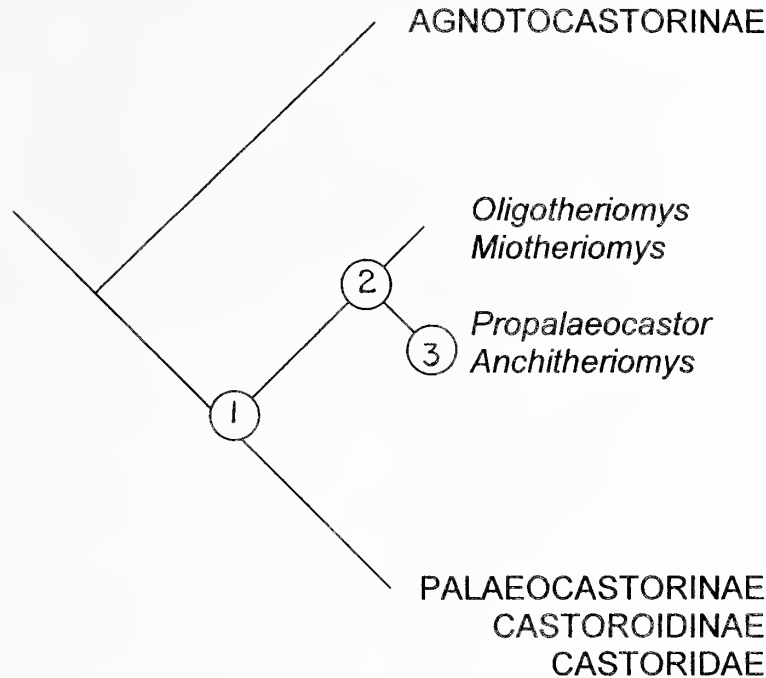


Fig. 4.—Cladogram of relationships of the subfamilies of castorids. Tree is based on phylogenetic analyses in the following studies: Korth and Emry (1997), Korth (2001c), and Korth and Rybczynski (2003). Explanation of nodes: 1, posterior divergence of upper tooth rows; last premolar larger than molars. 2, Anchitheriomyinae, greater complexity of occlusal surface of molars; posterior maxillary notch rather than foramen; shortened nasal bones; greatly reduced incisive foramen; zig-zag pattern of mandibular processes. 3, ridged incisors. For all other nodes see Korth and Emry, 1997:fig. 4; Korth, 2001c:fig. 4, table II; Korth and Rybczynski, 2003:fig. 6, table 3.

posteriorly. Posterior to it is a small, circular accessory fossettid on the lingual half of the tooth. The mesofossettid is elongated and oriented directly buccolingually on the tooth. Posterior to the mesofossettid is another small, circular accessory fossettid near its buccal end. The metafossettid is not recognizable as such. There are two posterior fossettids; the lingual one is Y-shaped and oriented obliquely. Buccal to it is a small, oval fossettid.

Only the alveoli are preserved for the molars. All are three-rooted and only slightly smaller than P_4 .

Discussion.—UNSM 26598 is intermediate between the earlier *Oligotheriomys* and *Anchitheriomys* in size and crown height of the cheek teeth. It also maintains the primitive morphology of the lower incisor with a smooth enamel surface. However, there are a few characters of the mandible that separate it from all other anchitheriomyines. The position of the mental foramen is much higher than in any other anchitheriomyine and the ascending ramus arises more anteriorly than in other

anchitheriomyine except the Oligocene Eurasian genus *Propalaeocastor* (Lychev, 1970:fig. 1a; Hugueney, 1975:fig. 7). The crown height of the cheek teeth of UNSM 26598 is similar to that of *Propalaeocastor*; however, the latter has the distinctly ridged incisors that are also characteristic of *Anchitheriomys*, which are distinct from the anteriorly smooth incisor of UNSM 26598.

The occurrence of UNSM 26598 in the Hemingfordian further demonstrates the greatest diversity of anchitheriomyines in North America at that time. However, whereas *Anchitheriomys* is believed to be an immigrant taxon from Eurasia (Korth, 1998), UNSM 26598, because of its primitive incisor (smooth enamel surface), is not likely part of this immigration and may be directly derived from the earlier occurrence of anchitheriomyines (*Oligotheriomys*) in the Oligocene of North America.

RELATIONSHIPS OF THE ANCHITHERIOMYINAE

The Agnotocastorinae was first established to contain the earliest and most primitive species of castorids including *Anchitheriomys* (Korth and Emry, 1997). Later, the Anchitheriomyini was defined as a Tribe of the Agnotocastorinae (Korth, 2001c). However, the characters used to include the anchitheriomyines within the Agnotocastorinae appear to be primitive for beavers

(complex occlusal pattern of cheek teeth, procumbent incisors, elongated rostrum). Likewise, the characters of the anchitheriomyines that separated them from the remainder of the agnotocastorines (premolars larger than molars, tooth rows diverge posteriorly; reduced incisive foramen) were viewed as convergent on the more advanced castorids. It appears now that these latter

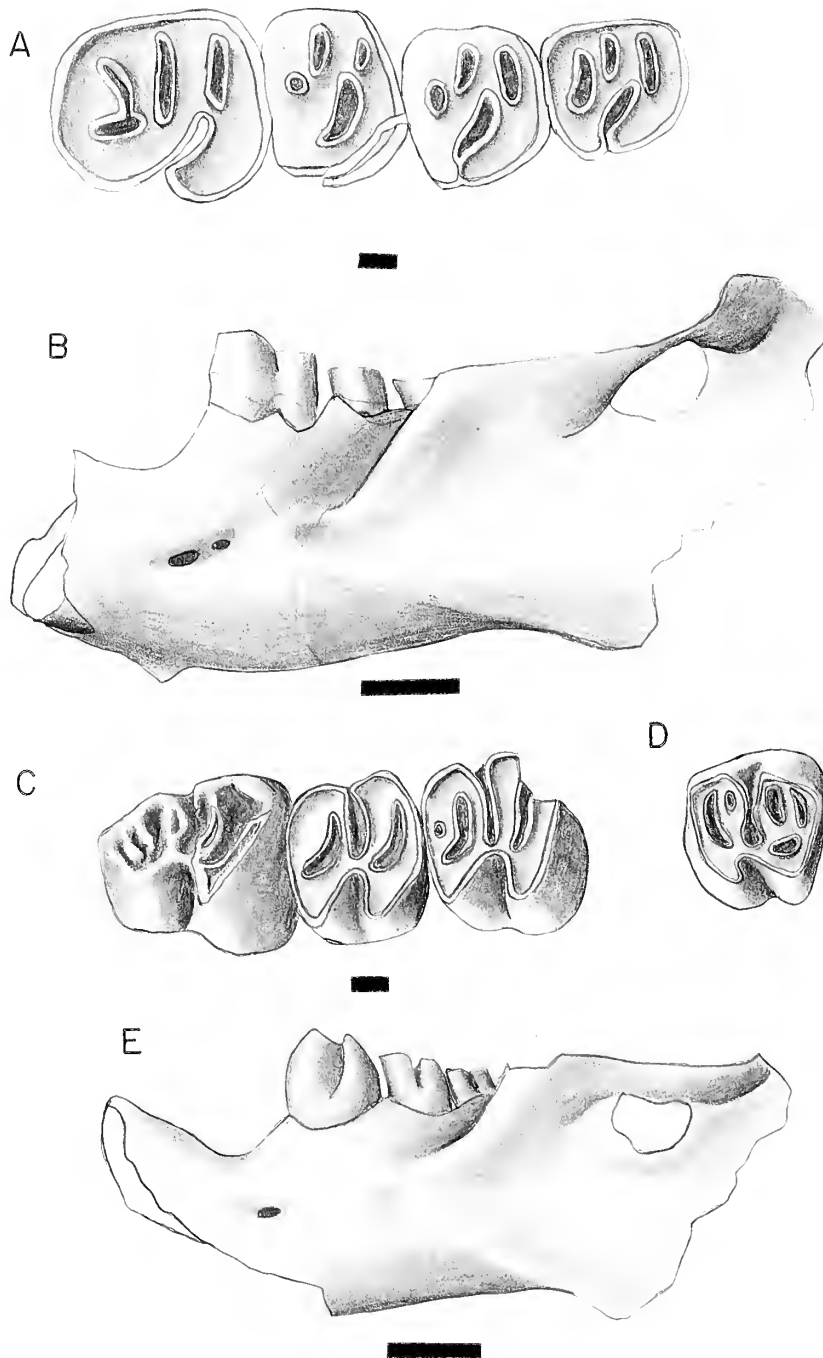


Fig. 5.—Dentition and mandibles of *Monosaulax baileyi* and *Enroxenomys wilsoni*. A and B, *Monosaulax baileyi*, UNSM 26707. A. P₄–M₃. B. lateral view of mandible. C–E, *E. wilsoni*. C. UNSM 26708, left P₄–M₂. D. UNSM 26710 left M¹. E. UNSM 26708, lateral view of mandible. Bar scale for teeth = 1 mm. Bar scale for jaw = 5 mm.

characters, while not as well developed as in the Castorinae, Palaeocastorinae and Castoroidinae, are shared, derived features that should unite the anchitheriomyines with these other subfamilies (Node 1:Fig. 4). In order to do this, the tribe Anchitheriomyini must be raised to level of subfamily. Autapomorphic features of the Anchitheriomyinae are: 1) greater complexity of occlusal

surface of molars; 2) posterior maxillary foramen open laterally (notch formed); 3) shortened nasal bones; 4) greatly reduced incisive foramen (even greater than in palaeocastorines, castorines and castoroidines); and 5) independent development of the zig-zag pattern of mandibular processes (Node 2:Fig. 4). The anchitheriomyines cannot be included in any of the more advanced

Table 3.—Dental measurements of *Monosaulax baileyi*. Abbreviations as in Table 1. Measurements in mm.

	UNSM#:	119818	119819	26707	119816	119817
P ₄ a-p		5.69	5.70	5.60	5.27	
P ₄ tra		4.05	3.82	3.85	2.95	
P ₄ trp		4.40	4.69	4.55	4.02	
M ₁ a-p				3.30	3.19	
M ₁ tr				4.25	3.73	
M ₂ a-p				3.00		
M ₂ tr				3.80		
M ₃ a-p				3.70		
M ₃ tr				3.05		
P ₄ -M ₃				16.20	16.15	16.49
I ₁ a-p				4.55		
I ₁ tr				4.05		
Length of diastema				—	14.26	13.38
Depth of mandible at M ₁				12.98	13.17	12.39

subfamilies because they lack many of the derived features that unite them (see Korth and Emry, 1997:fig. 4; Korth, 2001c:fig. 4, table II; Korth and Rybczynski, 2003:fig. 6, table 3).

Within the Anchitheriomyinae the latest and most derived genus is *Anchitheriomys*, which occurs in the Miocene of North America, Europe, and Asia (Stirton, 1935; Xu, 1994; Hugueney, 1999). Other than its much larger size, this genus is distinguished from others by its ridged incisors. The only other genus with this feature is the Eurasian Oligocene genus *Propalaeocastor* (Hugueney, 1975). Because of this, Korth (2001a) suggested that the anchitheriomyines originated in the Oligocene in North America (*Oligotheriomys*), then migrated to Asia where *Propalaeocastor* first occurs, then migrated back to North America in the early Miocene with the first occurrence of *Anchitheriomys* (three species, *A. senrudi*, *A. stouti*, and *A. nanus*).

Two additional species of anchitheriomyines are recognized here, *Miotheriomys stenodon* and the indeterminate species. These species maintain the primitive morphology of the incisor (smooth enamel surface) suggesting that they are not part of an immigration from Eurasia, but rather are derived directly from the North American Oligocene species of *Oligotheriomys*. There is still a considerable time gap between the latest occurrence of *Oligotheriomys* (Orellan) and the Hemingfordian species.

Subfamily Castoroidinae Allen, 1877

Tribe Castoroidini Allen, 1877

Monosaulax Stirton, 1935

Monosaulax baileyi, new species

(Fig. 5 A, B; Table 3)

Type Specimen.—UNSM 26707, left mandible with incisor and p₄-m₃.

Referred Specimens.—UNSM 119816, right mandible with p₄-m₃; UNSM 119817, right mandible alveoli for p₄-m₃; UNSM 119818 and 119819, isolated P₄s.

Table 4.—Dental measurements of *Euroxenomys wilsoni* from the Hemingfordian of Nebraska. Abbreviations as in Table 1. Measurements in mm.

	UNSM#:	26708	26709	26711	119813
P ₄ a-p		5.16	5.29	4.42	4.49
P ₄ tra		3.12	3.33	3.01	—
P ₄ trp		4.11	3.75	4.00	—
P ₄ crown height		5.86	—	—	—
M ₁ a-p		2.59	2.91	2.79	3.00
M ₁ tr		4.15	3.48	3.75	4.02
M ₂ a-p		3.73	3.00	3.10	3.69
M ₂ tr		3.69	3.30	—	3.80
M ₃ a-p					3.90
M ₃ tr					3.42
I ₁ a-p		3.90	3.22	—	
I ₁ tr		3.49	3.35	3.61	
P ₄ -M ₃		15.61	15.41	15.17	
Depth of mandible at M ₁		9.51	10.79	11.02	10.32
Length of diastema		9.44	11.59	13.20	11.00

UNSM#:	119821	119821
	(left)	(right)
P ⁴ a-p	4.01	3.82
P ⁴ tr	4.42	4.11

Horizon and Locality.—Holotype from UNSM locality Bx-7; referred specimens from localities Bx-7 and Bx-27, Runningwater Formation, Box Butte County, Nebraska.

Age.—Early Hemingfordian (early Miocene).

Diagnosis.—Large species (just slightly smaller than *M. pansus*); parafoissettid on P₄ forms a distinctive V-shape (gently curved on other species).

Etymology.—Patronym for Bruce E. Bailey, Highway Salvage Paleontologist of the University of Nebraska State Museum.

Description.—In size, *Monosaulax baileyi* is slightly smaller than *Monosaulax pansus*, the type species of the genus (Table 3; Korth, 2000b:table 1; Korth, 2002:table 2) and larger than all but the largest species, *M. skimmeri* (Evander, 1999:table 4). The mandible is similar to that of other species of *Monosaulax*. The mental foramen is doubled on the holotype but is only a single foramen on the two referred mandibles. The complete angle is not preserved on any of the specimens, but it is evident on the holotype and UNSM 119817 that the zig-zag arrangement of the mandibular processes characteristic of castoroidines is present. The lower incisor is, likewise, similar to that of other species of *Monosaulax*. The tooth is relatively wide with a smooth, gently convex anterior enamel surface.

The parafoissettid on P₄ forms a V-shape with the apex pointed posteriorly. In all other species of the genus, the parafoissettid is either straight or gently curved (concave anteriorly). The mesofossettid and metafoissettid are transversely elongated enamel lakes.

The molars are markedly smaller than P₄. The occlusal morphology of the lower molars is primitive for castoroidines, preserving three fossettids (para-, meso-, metafoissettid) with no signs of the more advanced S-pattern of *Eucastor* and later castoroidines.

Discussion.—The material referred here is clearly that of *Monosaulax* and not an agnotocastorine because it has a number of derived castoroidine features: 1) shorter diastema; 2) P₄ much larger than molars; 3) no irregularities on the fossettids of the cheek teeth; 4) arrangement of mandibular processes; and 5) wide, gently

anteriorly convex lower incisor. *Monosaulax baileyi* can be distinguished from other species of the genus by its size and the unique shape of the parafovea on P₄. Species of *Monosaulax* have been separated on the crown height of the cheek teeth and depth of lingual striations on P₄ (Korth, 1999). However, all of the specimens referred to *M. baileyi* are at least moderately worn, and so the total height of the crowns of the cheek teeth cannot be measured.

This is the earliest definite record of *Monosaulax* from North America. Emry and Eshelman (1998) cited isolated teeth of *Monosaulax* from the Hemingfordian of Delaware, but the material is too poor for a definite identification.

Tribe Trogontheriini Lychev, 1973

Euroxenomys Samson and Radulesco, 1973

Euroxenomys wilsoni Korth, 2001b

(Fig. 5C–E; Table 4)

Monosaulax nr. *M. curtus*, Galbreath, 1953.

Monosaulax, n. sp. Wilson, 1960.

Referred Specimens.—UNSM 26708, 26709, 26711, and 119813, mandibles with cheek teeth; UNSM 119820, isolated dP₄; UNSM 26710, left partial maxilla with M¹; and UNSM 119821, two isolated P⁴s and an incisor fragment.

Horizon and Locality.—All referred specimens from UNSM localities Bx-7 (Box Butte County), Sh-101B (Sheridan County), and Cr-169 (Cherry County), Runningwater Formation, Nebraska.

Age.—Early Hemingfordian (early Miocene).

Discussion.—The mandible and dentition of this species from northeastern Colorado have been fully described (Galbreath, 1953; Wilson, 1960; Korth, 2001b). The referred Nebraska material does not differ from that of the topotypic material from Colorado in size or morphology (Table 4).

The recognition of this species from Nebraska increases its temporal and geographic range. Previously, it was only known from the type material from the late Hemingfordian of northeastern Colorado (Galbreath, 1953; Wilson, 1960).

CONCLUSIONS

Previously, the record of fossil beavers from the Hemingfordian of North America was poor, being represented by four species (only one from Nebraska). All of these species except *E. wilsoni* are represented either by a single specimen or a few isolated teeth. The castorids reported here from the early Hemingfordian of Nebraska demonstrates a greater diversity than previously known.

The Arikareean record of beavers in North America is dominated by the Palaeocastorinae (as many as 14 species) with only a single species of agnotocastorine recognized (Martin, 1987; Korth, 1994; Xu, 1996). The Barstovian is dominated by castoroidine beavers (*Monosaulax* and *Encastor*) with only a single species of *Anchitheriomys* and possibly a species of the agnotocastorine *Hystricops* (Voorhies, 1990b). Unlike both the earlier Arikareean and later Barstovian, the Hemingfordian anchitheriomysines are the most diverse group of the

castorids. Four species and two genera (and possibly a third) of anchitheriomysines are known from the Hemingfordian of Nebraska. At no other time is there more than a single species of anchitheriomysine except in the Orellan where there are possibly two (Korth, 1998, 2000a).

Through the middle Tertiary of North America there is a distinct change in the castorid fauna. From Chadronian through Whitneyan times, the Agnotocastorinae are the most diverse group of castorids. In the Arikareean, the Palaeocastorinae are the most diverse. In the Hemingfordian, the greatest diversity is among the Anchitheriomysinae, and in the Barstovian and later, the Castoroidinae are by far the most diverse group of beavers until the extinction of the subfamily in the Pleistocene.

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A LATE TRIASSIC DROMATHERIID (SYNAPSIDA: CYNODONTIA) FROM INDIA

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ABSTRACT

A dromatheriid non-mammalian cynodont, *Rewaconodon tikiensis*, gen. et sp. nov., is described on the basis of several isolated teeth from the Late Triassic (Carnian) Tiki Formation, south Rewa Gondwana Basin, Madhya Pradesh, India. The new taxon, characterized by mediolaterally compressed tricuspid and tetracuspid postcanines with incipient root division, is similar to dromatheriids from the Late Triassic of Europe and North America. It also bears some plesiomorphic resemblance to *Therioherpeton* of Brazil. The new taxon further extends the geographic range of the already widespread distribution of dromatheriids and putatively related taxa. It corroborates the hypothesis on the cosmopolitan nature of the Late Triassic terrestrial vertebrate faunas worldwide. Because of the limited known materials and plesiomorphic features, the phylogenetic relationships of dromatheriids to mammals remain uncertain.

KEY WORDS: Dromatheriidae, Cynodontia, Tiki Formation, Late Triassic, India

INTRODUCTION

Dromatheriids are small to medium-sized carnivores of Late Triassic age. This group of non-mammalian cynodonts ("mammal-like reptiles") were previously reported from North America (Emmons, 1857; Sues et al., 1994; Sues, 2001), central and western Europe (Hahn et al., 1984, 1994; Godefroit, 1997; Godefroit and Battail, 1997; Godefroit et al., 1998). *Therioherpeton*, a cynodont considered by some to be closely related to dromatheriids (Battail, 1991), is known from Brazil (Bonaparte and Barberena, 1975, 2001).

Although first thought to be mammals in the 19th century (Emmons, 1857; Osborn, 1886), dromatheriids have been considered non-mammalian cynodonts since the 1920s (Simpson, 1926; Battail, 1991; Hahn et al., 1994; Sues, 2001). Sues (2001) reviewed the latest evidence and concluded that the "mammal-like" features of dromatheriids are shared by many non-mammalian cynodonts, and that dromatheriids are best regarded to be advanced non-mammalian cynodonts, rather than mammals. Because dromatheriids are represented as yet only by very incomplete fossils, there has not been a parsimony analysis of their relationships to other advanced cynodonts. Several workers placed dromatheriids in the Chiniquodontioidea (Carroll, 1987; Sigogneau-Russell and Hahn, 1994). Within this grouping, Battail (1991) suggested that dromatheriids are the sister-taxon to *Therioherpeton*. However, the currently available evidence, primarily from isolated teeth, is insufficient for assessing these problems (Sues, 2001). Certainly dromatheriids are

no more closely related to mammaliaforms than are tritheledontids (Battail, 1991; Bonaparte and Barberena, 2001), or possibly more distant from mammals than both tritheledontids and tritylodontids (Luo et al., 2002).

The composition of the family Dromatheriidae is also uncertain. The species of the type genus *Dromatherium* is from North America (Emmons, 1857; Simpson, 1926). The best represented taxon of this group is *Microconodon tenuirostris* (including "*Dromatherium tenuirostris*" of Emmons, 1857), as recently described in detail by Sues (2001). *Pseudotricouodon wildi* and *Tricuspes* from continental Europe have been placed in the Dromatheriidae (Hahn et al., 1984, 1994; Godefroit and Battail, 1997). However, the assignment of other taxa is questionable. Hahn et al. (1984) included in the Dromatheriidae *Therioherpeton* from Brazil (Bonaparte and Barberena, 1975); but this taxon was subsequently re-assigned by Kemp (1982) to tritheledontids. Battail (1991) also removed *Therioherpeton* from Dromatheriidae, but made it the sister-taxon to Dromatheriidae. Most recently, Bonaparte and Barberena (2001) considered *Therioherpeton* to be the sister-taxon to the clade comprising tritheledontids and mammaliaforms. Hahn et al. (1994; see also Godefroit and Battail, 1997) also assigned *Meurthodon* to Dromatheriidae. Shapiro and Jenkins (2001) noted that *Meurthodon* is too different in its fully divided roots from other dromatheriids and argued that it should not be placed in the Dromatheriidae. Lucas and Oakes (1988) erected "*Pseudotricouodon*" *chatterjeei* on

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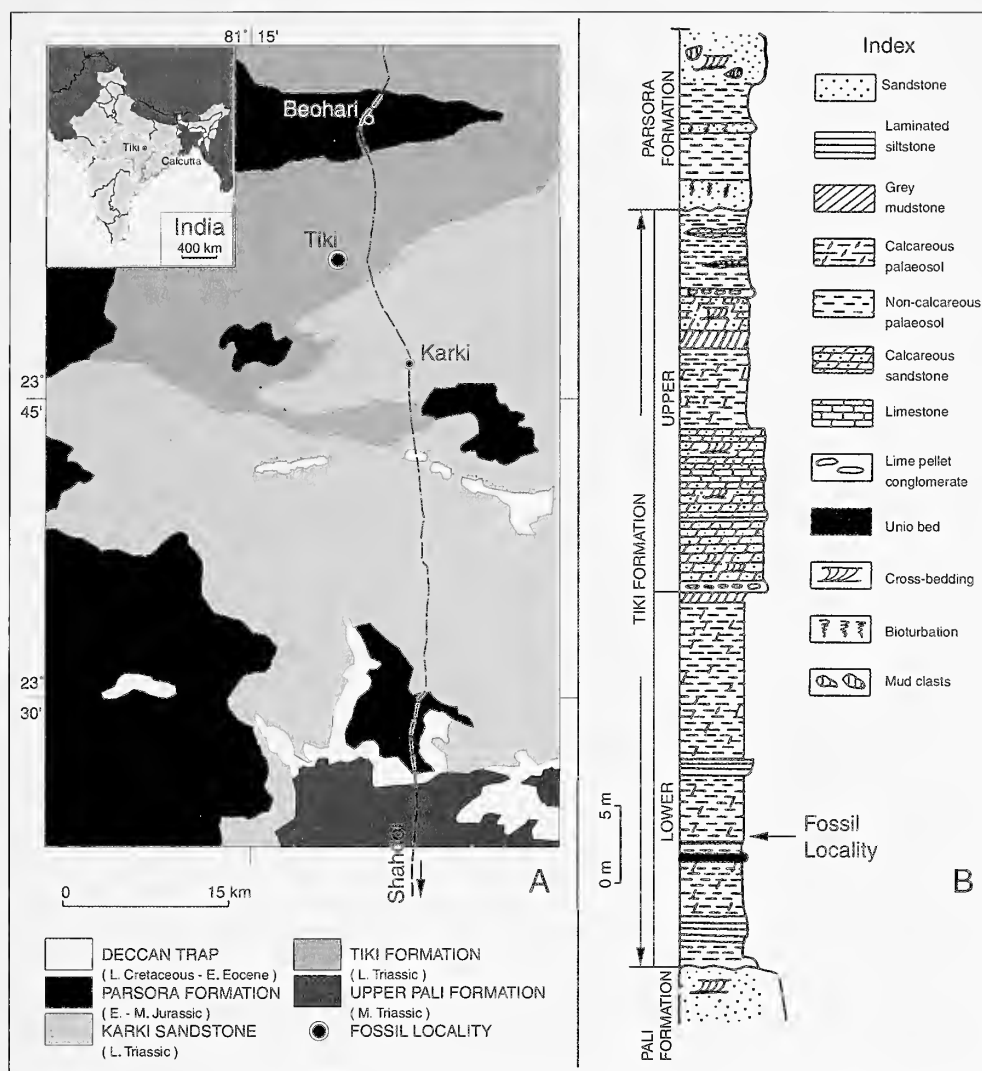


Fig. 1.—A. Simplified geological map of the fossil locality near the Tiki village, Madhya Pradesh State, India. B. The lithostratigraphic section of the Tiki fossil locality (Tiki Formation, the Gondwana Supergroup).

the basis of a specimen from the Upper Triassic of New Mexico, but the assignment of this specimen to *Pseudotriconodon* has been recently questioned (Sues, 2001). In this study, we assume the most conservative

membership for dromatheriids: *Dromatherium*, *Microconodon*, *Pseudotriconodon wildi*, *Tricuspes* and the new taxon from the Upper Triassic (Carnian) Tiki Formation of India to be described below.

STRATIGRAPHY

The dromatheriid and other non-mammalian cynodont material reported here was collected during the field work of 1997–98 and 1998–99 from an exposure of the calcareous, red mudstones of the Tiki Formation four km southwest of Tiki village in the south Rewa Gondwana Basin, Madhya Pradesh State, India (Fig. 1A). The Tiki formation in the south Rewa Gondwana Basin comprises red mudstone with greenish-gray mottling, calcareous sandstone, cross-bedded feldspathic sandstone and a few lime pellet conglomerate horizons (Fig. 1B).

The Tiki Formation is a part of the Upper Gondwana Group. In the south Rewa Basin it is underlain by the Pali Formation with a local erosional contact. Floral assemblage in the upper part of Pali Formation indicates an Early to Middle Triassic age (Tarafder et al., 1993). The Tiki Formation is unconformably overlain by the Parsora Formation, the lower part of which comprises mudstone of pink, red and lavender colors, brownish ferruginous silty shale and interbeds of sandstone containing clay clasts of varying sizes. The palynomorph evidence

suggests a Rhaetic to Liassic age for the Parsora Formation (Roy Chowdhury et al., 1975; Tarafder et al., 1993).

The Tiki Formation is rich in fossil vertebrates and palynomorphs, which helped to establish its biostratigraphic correlation. The vertebrate assemblage of the Tiki Formation includes: the temnospondyl *Metoposaurus maleriensis* (Sengupta, 1992), the phytosaur *Parasuchus hislopi* (Chatterjee, 1978), the rauisuchid *Tikisuchus romeri* (Chatterjee and Majumdar, 1987) and the rhynchosaur *Hyperodapedon huxleyi* (Benton, 1983). Recently, a primitive morganucodontid mammal *Gondwanadon tapani*, represented by a molar, was discovered from the lower part of the Tiki Formation (Datta and Das, 1996). This vertebrate assemblage, except for the mammalian fossil, is virtually identical to the assemblage of the Maleri Formation of the Pranhita–Godavari valley in the Andhya Pradesh State, another well-known vertebrate-bearing horizon in the Triassic of India.

For intercontinental correlation, the fauna and flora of Tiki Formation can be correlated with the vertebrate fauna of Camp Springs member of the Dockum Formation (Hunt and Lucas, 1991a, b; Chatterjee, 1986; Kutty and Sengupta, 1989), also termed the “North American Land Vertebrate Faunachron A” (Lucas and Hunt, 1993) or Otischalkian (Lucas, 1998). Palynomorphs from the Tiki Formation are closely comparable to the Onslow palynoflora of northwestern Australia (Maheshwari and Kumaran, 1979). This stratigraphically informative

palynomorph assemblage from the Tiki Formation consists of *Aulisporites artigmus*, *Cannosporites secatus*, *Duplicisporites granulatus*, *Granuloparculariipoliis* sp., *Enzonalasporites densus*, *E. ignacii* and *E. vigenus*. This palynofloral composition is similar to that of the upper part of the *Samaropollenites speciosus* Zone of the Onslow palynoflora in Australia. The latter has been dated as Carnian (Maheshwari and Kumaran, 1979). The megaf flora of the Late Triassic of Indian Peninsula is not sufficiently known for intercontinental correlation (Anderson and Anderson, 1993).

Therefore the Tiki Formation, based on its faunal and floral assemblage, can be compared with the Maleri Formation in the Pranhita–Godavari valley of India and the Carnian faunal assemblages in other non-marine strata elsewhere (Lucas, 1998). Lucas (1998) correlated the Maleri Formation to lower Carnian (Otischalkian of Lucas, 1998). Benton (1994) correlated the Tiki and Maleri Formations to the upper Carnian (Tuvanian), which he considered to be equivalent to the Schilfsandstein–Gipskeuper zonations of the German Keuper. Currently there are no magnetostratigraphic data for correlating the Tiki and Maleri Formations directly to the standard marine sequence.

Abbreviations: GSI, Geological Survey of India; Pal/CHQ, Palaeontological collections (“chiquodontoids”) of GSI in Calcutta. Cusps on postcanines are designated by letters A/a through E/e, following the alphabetical scheme by Crompton (1971, 1974).

MATERIALS AND METHODS

About 5 metric tons of matrix were collected from the calcareous, red mudstone beds of the Tiki Formation for screen washing. The clay was gradually removed by washing in water. The residue was screened, dried, and manually sorted under a microscope. This procedure has yielded a large number of isolated teeth of ornithischian dinosaurs, phytosaurs, sphenodontians and some cynodonts. Nine teeth that can be referred to dromatheriids have been recovered. Of the nine, eight postcanines described here are considered to belong to a single taxon, whereas the remaining one is distinctly different.

The determination of the relative position of a tooth in the postcanine row is by comparison to the better fossils of *Microconodon* (Sues, 2001). For orientation of the isolated cynodont postcanines, we follow the criteria used by many previous workers, as summarized by Godefroit and Battail (1997). The more convex side is conventionally and arbitrarily regarded as the labial side for both upper and lower postcanines. As the cusp inclination is always distal, if present, the direction of cusp inclination is regarded as distal.

If a contact wear facet is developed, it develops on the labial side of the lower postcanines and on the lingual side of the uppers. Dental contact wear can only develop if the dental replacement rate is sufficiently slow and the upper and lower postcanines have one-to-one opposition (Luo, 1994). These features are absent in most non-mammalian cynodonts, except for such derived taxa as the Gomphodontia (Crompton, 1972), tritheledontids (Gow, 1980) and tritylodontids (Sues, 1986). More common for the carnivorous non-mammalian cynodonts are apical abrasion of cusps. Because the lower teeth always occlude on the lingual side of the upper, the apical abrasions tend to spread from the apex and its associated crest to the occlusal (“contact”) side of the cusp. The apical abrasion of cusps on a tooth is consistently slanted toward the occlusal side of the tooth: the labial side for the lower and the lingual side for the upper. Presence of these wear and abrasion patterns can be utilized for orienting some of the isolated teeth in this sample, for the purpose of description. The orientation of isolated carnivorous cynodont teeth needs to be verified by comparison to the *in situ* teeth in the jaws when better preserved fossils become available.

SYSTEMATIC PALEONTOLOGY

Clade Cynodontia Owen, 1861
Family Dromatheriidae Gill, 1872
Genus *Rewaconodon* gen. nov.

Etymology.—The genus is named after the Rewa Gondwana Basin of the Madhya Pradesh State, India.

Diagnosis.—Postcanine teeth characterized by labiolingually compressed triconodont-like crown with three to

four cusps aligned in a longitudinal row; incipient division of the root(s) by shallow grooves or depressions on both the lingual and the labial sides of the root(s) and two portions of the root are connected by a thin sheet of dentine. Apical abrasion is developed on at least some cusps on all of the postcanines. Fewer teeth also have occlusal wear between the main cusp and the two

Table 1.—Measurements of postcanine teeth of *Rewaconodon tikiensis* (Dromatheriidae, Cynodontia) from the Late Triassic (Carnian) Tiki Formation of south Rewa Gondwana basin, Madhya Pradesh, India.

	GSI Pal/CHQ001	GSI Pal/CHQ002	GSI Pal/CHQ003	GSI Pal/CHQ004	GSI Pal/CHQ005	GSI Pal/CHQ006	GSI Pal/CHQ007	GSI Pal/CHQ008
Number of cusps	3	3	3	3	4	4	4	4 + cingulid cusps f
Main cusp a height (mm)	1.03	0.78	0.80	0.50	1.18	Not available	0.88	0.80
Cusp c height (mm)	0.30	0.28	0.50	0.38	0.65	0.55	0.35	0.60
Cusp b height (mm)	Not available	0.15	0.35	0.35	0.55	0.33	0.28	0.30
Cusp d height (mm)	—	—	—	—	0.25	0.23	0.13	Not available
Tooth length (mm)	0.93	0.90	0.80	0.85	1.20	1.13	0.85	1.13
Tooth width (mm)	0.42	0.31	0.38	0.31	0.27	0.44	0.22	0.29

accessory cusps of the crown. There is no bulging cingulum near the base of the crown, or a constriction at the crown–root junction. *Rewaconodon* differs from the morganucodontid *Gondwanadon* from the same site in having much smaller cusps c and d. *Rewaconodon* differs from chiniquodontids and probainognathians in that the primary cusp of its postcanines is not as recurved distally as in the latter groups. It differs from thrinaxodontids, chiniquodontids and probainognathians in having a more conspicuous (but still incomplete) division of the postcanine roots (Romer, 1969a, b; 1970; Hopson and Kitching, 2001; Abdala, 2000; Abdala and Giannini, 2002). It differs from *Meurthodon* and *Mitrodon* in lacking the complete root divisions in the tetracuspoid postcanines and in being much smaller in size (Sigogneau-Russell and Hahn, 1994; Shapiro and Jenkins, 2001); differs from the multi-cuspoid, and multi-rowed postcanines of diademodontids, traversodontids, and tritylodontids (Crompton, 1972; Sues, 1986); differs from thrinaxodontids, *Prozostrodon* and tritheledontids in lacking the well-developed cingulids; differs from tritheledontids and *Riograndia* in having fewer cusps on the lower postcanines (Bonaparte and Barberena, 2001; Bonaparte et al., 2001). Among all non-mammalian cynodonts, *Rewaconodon* is most similar to *Therioherpeton* and the dromatheriids *Tricuspes* and *Microconodon*. Yet *Rewaconodon* is much smaller (Table 1). Its postcanines are 50% of those of *Therioherpeton*, 50–60% of those of the European dromatheriid *Tricuspes* and *Pseudotriciconodon* (Godefroit and Battail, 1997), 70–80% of the teeth of North American dromatheriid *Microconodon*, with exception of one juvenile specimen, as reported by Sues (2001).

Rewaconodon differs from *Therioherpeton* and *Microconodon* in that the individual cusps are more stout (less compressed) in cross-section (Bonaparte and Barberena, 1975; Sues et al., 1994); differs from *Tricuspes* in lacking a constricted waist on the mesial aspect of cusp b and the distal aspect of cusp c (Hahn et al. 1994); differs from *Pseudotriciconodon* in that the root division is either confined to the tip of the root, or more often completely missing in *Pseudotriciconodon*; differs from *Charruodon*, a South American therioherpetid, and *Lepagia*, a Europe-

an cynodont of uncertain affinities, in lacking the shallow constriction between the crown and root found in the latter taxa (Sigogneau-Russell and Hahn, 1994; Abdala and Ribeiro, 2000).

Rewaconodon tikiensis gen. et sp. nov.

Etymology.—The species is named after the village Tiki in the Shadol district, Madhya Pradesh, India (Geological Survey of India topo map No. 64 E) (Figure 1A).

Holotype.—GSI Type No. Pal/CHQ-005 (Figure 2), a tetracuspoid lower postcanine tooth, in the collection of the Curatorial Division, Geological Survey of India, Calcutta, India.

Referred specimens.—GSI Type Nos. Pal/CHQ-001, Pal/CHQ-002, Pal/CHQ-003, Pal/CHQ-004, Pal/CHQ-006, Pal/CHQ-007 and Pal/CHQ-008. For measurements of these teeth see Table 1.

Diagnosis.—As for the genus.

Type Locality and Type Stratum.—Lower part of Tiki Formation of the Gondwana Supergroup (Figure 1B); Late Triassic (Carnian); 4 km southwest of the Tiki village (Latitude 23°55'N; Longitude 81°22'E), south Rewa Gondwana Basin, Madhya Pradesh State, India.

DESCRIPTION

Four tricuspid postcanines (GSI-Pal/CHQ-001 through Pal/CHQ-004) are interpreted as anterior postcanines, by comparison to those of *Microconodon* (Sues, 2001). Pal/CHQ-001 (Figure 3) is a “premolariform” positioned in the anterior part of the postcanine row. Following the criteria of Godefroit and Battail (1997), we tentatively interpret it as an upper right anterior postcanine. Its principal cusp A has a longer mesial crest than the distal crest. The small and more distal cusp C is raised beyond the crown–root junction. The mesial accessory cusp (B?) is much smaller and lower than the distal cusp C. The crown enamel is smooth; some distinctive, vertical wrinkles are present on both the lingual and labial sides near the base of the main cusp. Main cusp A and distal cusp C show apical abrasion.

One tricuspid tooth (Pal/CHQ-002; Figure 4) is considered to be a lower right anterior postcanine. Main

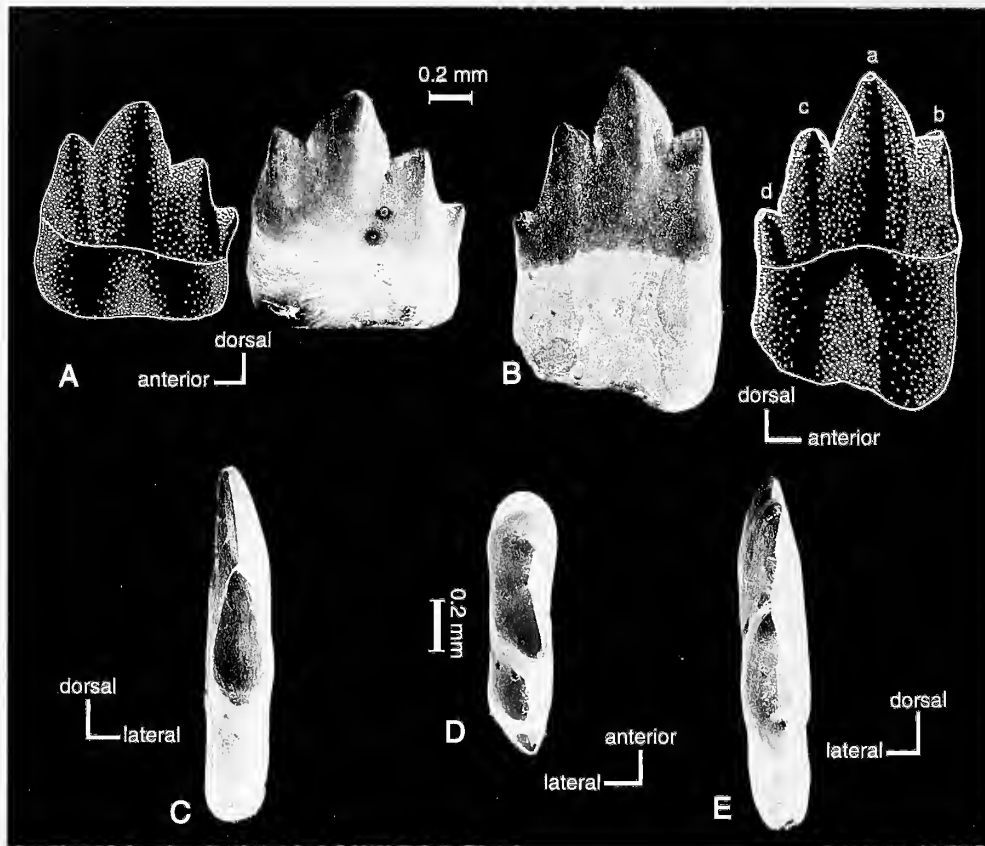


Fig. 2.—Holotype of *Rewaconodon tikiensis* (GSI Pal/CHQ-005; Dromatheriidae, Cynodontia). SEM photographs of a lower left posterior tetracuspoid postcanine: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, dorsal (occlusal) view. E, posterior (distal) view. Cusp designation following Crompton (1974).

cuspid a is the largest cusp. Its mesial crest is slightly more convex than the distal crest. Accessory cusps b and c are arranged almost symmetrically relative to cuspid a. There is no cingulid at the base of the crown or constriction at the crown-root junction. The root is incipiently divided by a furrow on both lingual and labial sides; the two portions of the root are connected by dentine such that in the horizontal section the root forms a figure 8. A tricuspid tooth (Pal/CHQ-003; Figure 5) is an upper right postcanine. This tooth differs from other tricuspid teeth in having much larger mesial and distal accessory cusps. The crown of Pal/CHQ-004 (Figure 6) is symmetrical labiolingually and has a similar curvature on both sides; its crown is extensively damaged. Thus its orientation is uncertain.

The four tetracuspoid teeth (GSI-Pal/CHQ-005 to 008) are considered to be the posterior postcanines by comparison to those of *Microconodon* (Sues, 2001), *Therioherpeton* (Bonaparte and Barberena, 1975, 2001) and, to a lesser extent, to *Mitrodon* (Shapiro and Jenkins, 2001). The holotype specimen (GSI-Pal/CHQ-005; Figure 2) is a posterior lower postcanine from the left side, following the morphological criteria of orienting the

isolated cynodont postcanine teeth by Godefroit and Battail (1997). Primary cuspid a is labiolingually compressed and slightly recurved, with mesial and distal crests extending from the apex. Mesial cuspid b has a rounded mesial face, and a distal crest extending from the apex. Distal cuspid c is lower than mesial cuspid b. The distal cuspidule d is the smallest of the four cusps. Two wear facets are present on the labial side of the crown, one in the valley between cusps b and a and the other between cusps a and c. The enamel surface near the crown and root junction slightly bulges, but there is no distinctive cingulid or constriction to separate the enamel surface of the crown from the dentine surface of the root.

Two tetracuspoid teeth (Pal/CHQ-007, 008; Figure 7) are also likely to be left lower posterior postcanines, but both show a more mesio-distal asymmetry than the holotype specimen. Principal cuspid a of both teeth is the largest cusp. Its mesial crest is much longer than the distal crest, making the cusp appear slightly recurved. Distal cuspid c is only slightly lower than and in close proximity to cuspid a. Mesial cuspid b is much smaller than d. Distal cuspid d is variable: well developed in the type specimen (Pal/CHQ-005), but small in one specimen (Pal/CHQ-007),

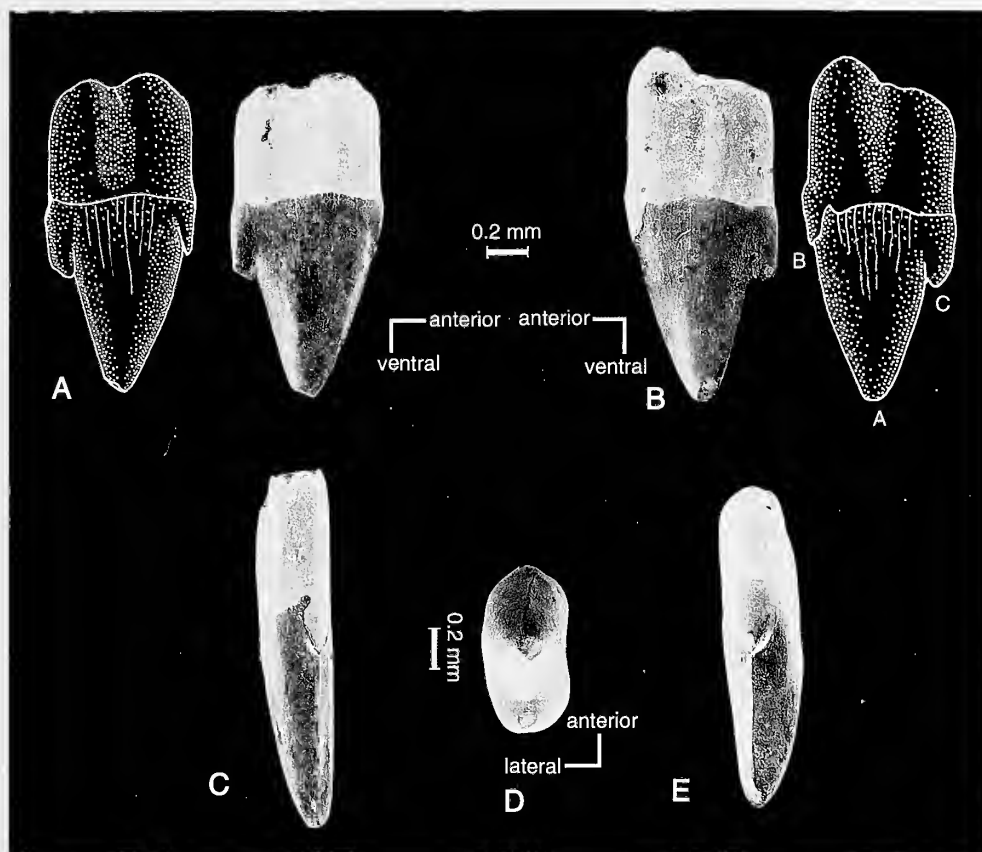


Fig. 3.—*Rewaconodon tikiensis* (GSI Pal/CHQ-001: Dromatheriidae, Cynodontia). An upper, premolariform (anterior) postcanine from right side: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, crown (occlusal) view. E, posterior (distal) view.

and vestigial in the other (Pal/CHQ-008). Another variable feature is anterolabial cingulid cuspule f (after alphabetical designation of Crompton, 1974), only present in Pal/CHQ-008 but absent in other tetracuspoid teeth. All tetracuspoid teeth have developed some degree of apical abrasion at the tips of the tooth cusps.

We tentatively interpret Pal/CHQ-006 (Figure 8) as a lower right postcanine near the middle of the tooth row because it is much wider and slightly shorter than other tetracuspoid teeth, fitting the profile of the “middle” postcanines in tooth row of some advanced cynodonts (Osborn and Crompton, 1971). Pal/CHQ-006 has much smaller cusps b and c than other tetracuspoid teeth. Cusp b is positioned at the mesial end of the tooth near the cingulid level, and is less distinctive than the same cusp in other tetracuspoid teeth.

DISCUSSION

Taxonomy.—The morphological and size differences of *Rewaconodon* from other dromatheriids and the wide geographic separation of the Tiki locality from the localities in North America and Continental Europe make it reasonable for us to recognize *Rewaconodon tikiensis*

gen. et sp. nov. as a new taxon of the Dromatheriidae. All the specimens come from the same locality of the Tiki Formation, and have a relatively narrow range of variation in crown and root structure. The morphological variation among the teeth can be attributed to different positions in the tooth-row. Therefore we assign these teeth to a single taxon *R. tikiensis*. More detailed taxonomic justifications are given below.

The postcanines of *Rewaconodon* have a suite of primitive dental characters of advanced non-mammalian cynodonts. Among the known non-mammalian cynodont groups of the Late Triassic, *Rewaconodon* are most similar to *Microconodon* of North America (Simpson, 1926; Sues, 2001) and *Tricuspes* of Europe (Hahn et al. 1994; Godefroit and Battail, 1997), and to a lesser extent to *Pseudotricodon* of Europe (Hahn et al., 1984, 1987; Sigogneau-Russell and Hahn, 1994). Nonetheless, *Rewaconodon* can be unambiguously distinguished from all other taxa hitherto placed in the Dromatheriidae (Hahn et al., 1994: fig.2). It differs from *Microconodon*, *Dromatherium*, and *Lepagia* in having vertical wrinkles (striations) on the enamel near the base of the principal cusps of the tricuspoid teeth, and in having smaller teeth (see “diagnosis” and Table 1).

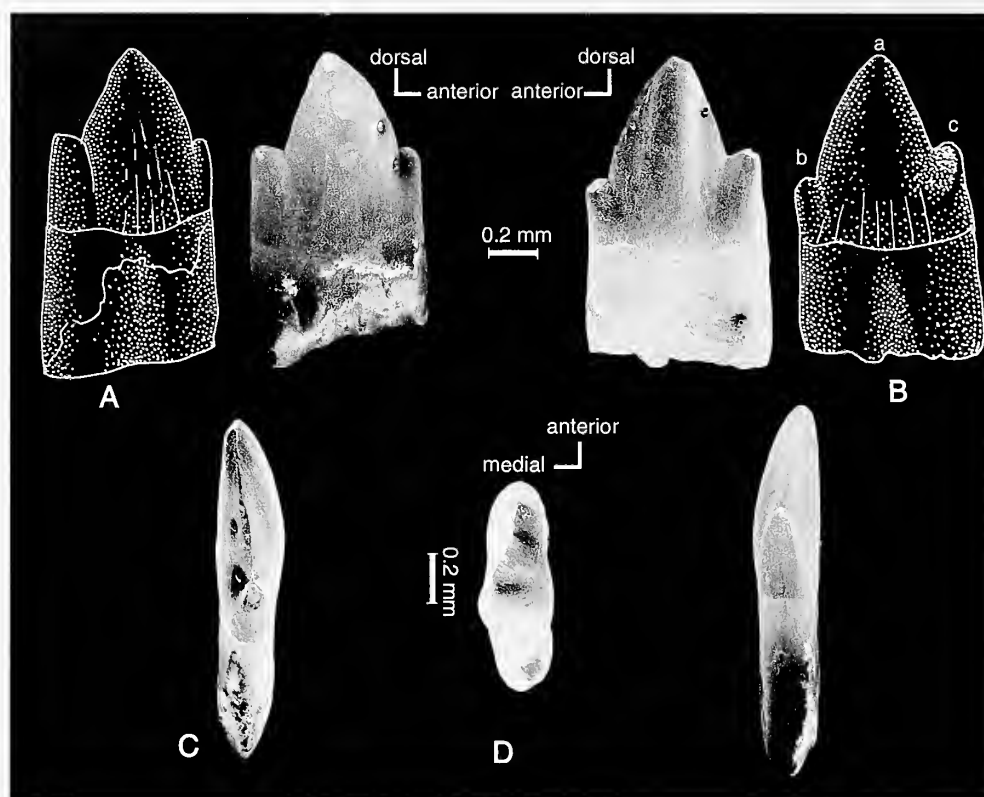


Fig. 4.—*Rewaconodon tikiensis* (GSI Pal/CHQ-002; Dromatheriidae, Cynodontia). Lower right anterior postcanine: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, crown (occlusal) view. E, posterior (distal) view.

All eight cynodont teeth collected from the Tiki sites have essentially a “triconodont-like” design, with three or four labiolingually compressed cusps in a straight alignment. This sample also shows a relatively narrow range of size variation. The length of the crown ranges from 0.80 mm to 0.93 mm for the tricuspid teeth, and 0.85 mm to 1.20 mm for the tetracuspid teeth. The height of the crown varies from 0.50 mm to 1.03 mm for the tricuspid teeth, from 0.70 mm to 1.18 mm for the tetracuspid teeth (Table 1). These teeth of *Rewaconodon tikiensis* are smaller than those currently known in *Microconodon* and other dromatheriids.

The morphological variation of the tricuspid and tetracuspid postcanines corresponds, in some degree, to the gradient variation along the postcanine series, as commonly seen in many (but not all) advanced non-mammalian cynodonts (e.g., Osborn and Crompton, 1971). *Microconodon* shows an increase in cusp number and more equal size of cusps in the more posterior teeth (Sues, 2001). It is likely that more than one generation of replacement teeth are represented in this sample; so some of the morphological variation may be related to the differences between successive generations of teeth at the same tooth locus.

For practical purposes of separating the taxa of this family from other advanced non-mammalian cynodonts,

there is a combination of plesiomorphic tooth crown features of the postcanines, such as the absence of basal constriction at the crown-tooth junction. Current evidence for supporting the monophyly of this family is quite limited; therefore the validity of the Dromatheriidae must be tested when better fossils become available in the future. However, the limited dental characteristics are not sufficient for resolving the complex relationships of dromatheriids to chiniquodontids, to *Meurthodon* and *Mitrodon*, and to *Riograndia*, *Therioherpeton*, and probainognathians, as already noted by several recent studies (Bonaparte and Barberena, 2001; Shapiro and Jenkins, 2001; Sues, 2001).

Dental morphology.—The wear patterns are highly variable among postcanines in this sample assigned to *Rewaconodon*. Six of the postcanines assigned show some degrees of apical abrasion, a primitive pattern of the carnivorous non-mammalian cynodonts. Irregular apical abrasion may be associated with more frequent dental replacements than the diphyodont dental replacement as the teeth with less frequent replacement tend to have precise match of the crown but less irregular abrasion. The presence of apical abrasion does not mean that the upper and lower postcanines have a one-to-one occlusal contact. Several postcanines show that the apical abrasion of a late stage can spread from apices to the occlusal

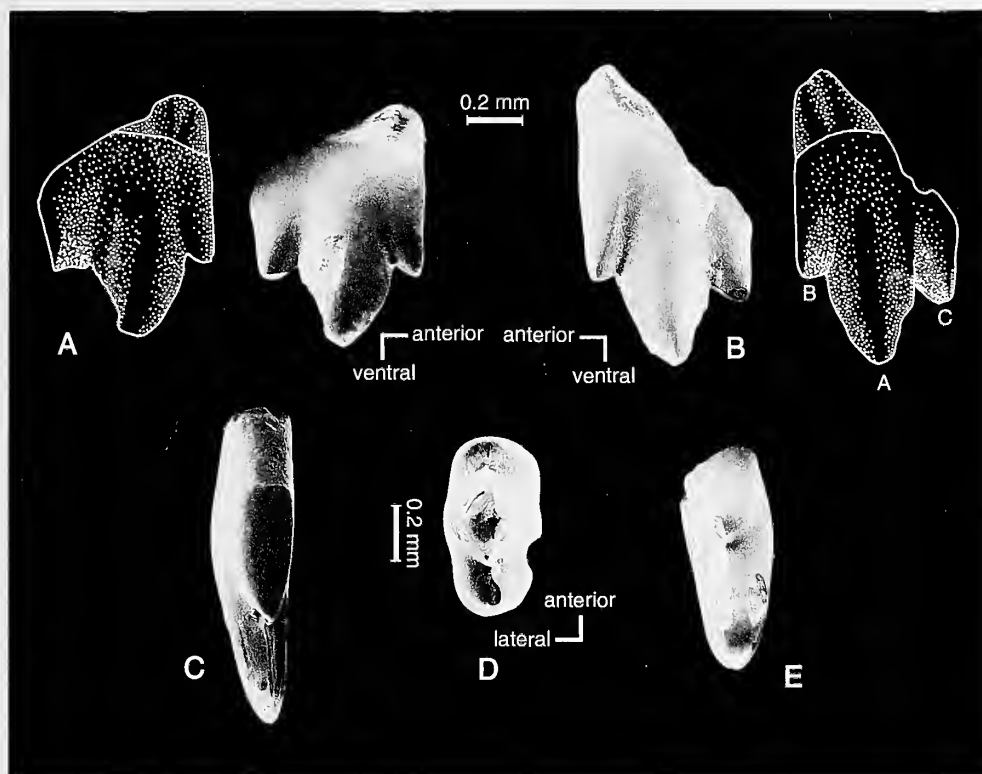


Fig. 5.—*Rewaconodon tikiensis* (GSI Pal/CHQ-003; Dromatheriidae, Cynodontia). Upper right anterior postcanine: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, crown (occlusal) view. E, posterior (distal) view.

contact surfaces on the cusps (e.g., Pal/CHQ-003, Pal/CHQ-004, Pal/CHQ-007, Pal/CHQ-008: Figures 5, 7 and 8).

Two teeth of *Rewaconodon* show some limited development of occlusal wear in the valleys between the principal cusp a and mesial cusp b (Pal/CHQ-003, Pal/CHQ-005). This wear is similar to the early-stage wear facets of morganucodontans and kuehneotheriids, the two most primitive groups of mammaliaforms in which the wear-facets have constant topographic relations to the cusps (Mills, 1971, 1984; Crompton 1974). Development of constant wear facets requires that the upper and lower postcanines have a one-to-one correspondence. If wear facets are present, it would also suggest that the individual teeth had a longer functional life, which may in turn indicate slower tooth replacement (Luo, 1994). In several Rhaeto-Liassic mammaliaforms, the beveled facets develop after a substantial amount of enamel surface was removed by the initial wear (Crompton, 1974; Crompton and Jenkins, 1979; Crompton and Luo, 1993). In the current sample of teeth referred to *Rewaconodon*, this type of well-matched and beveled facets has not been observed. It should be noted that the derived occlusal wear facets (e.g., on Pal/CHQ-005) are not as common as the plesiomorphic apical abrasion that is present in all of the teeth assigned to *Rewaconodon*. The indirect evidence so far suggests that *Rewaconodon* probably lacked the

one-to-one opposition of the upper and lower teeth required for the extensive development of dental wear facets.

Wear facets can occur on the postcanines of derived carnivorous cynodonts, but their presence is not a consistent feature among these cynodonts. So far, only the tritheledontid *Pachygenelus* is known to have developed the wear facets on the postcanines, although wear facets were developed across several cusps and lack consistent correspondence to individual cusps as in mammals (Gow, 1980). In the more derived mammaliaform *Sinoconodon*, a limited amount of wear is present on some posterior molars, but these molars lack consistent correspondence to individual cusps due to the lack of one-to-one correspondence of the upper and the lower molars and possible replacements of the molariform postcanines (Crompton and Luo, 1993; Zhang et al., 1998). Development of apical abrasion is most likely a primitive feature among the advanced non-mammalian cynodonts and mammaliaforms because it occurs not only in *Rewaconodon*, *Pachygenelus* and morganucodontans, and but also in other derived non-mammalian cynodonts, although less frequently in the more plesiomorphic groups.

Division of the postcanine roots was traditionally viewed as a derived, mammal-like characteristic, as discussed by Kemp (1983; also Rowe, 1988; Wible,

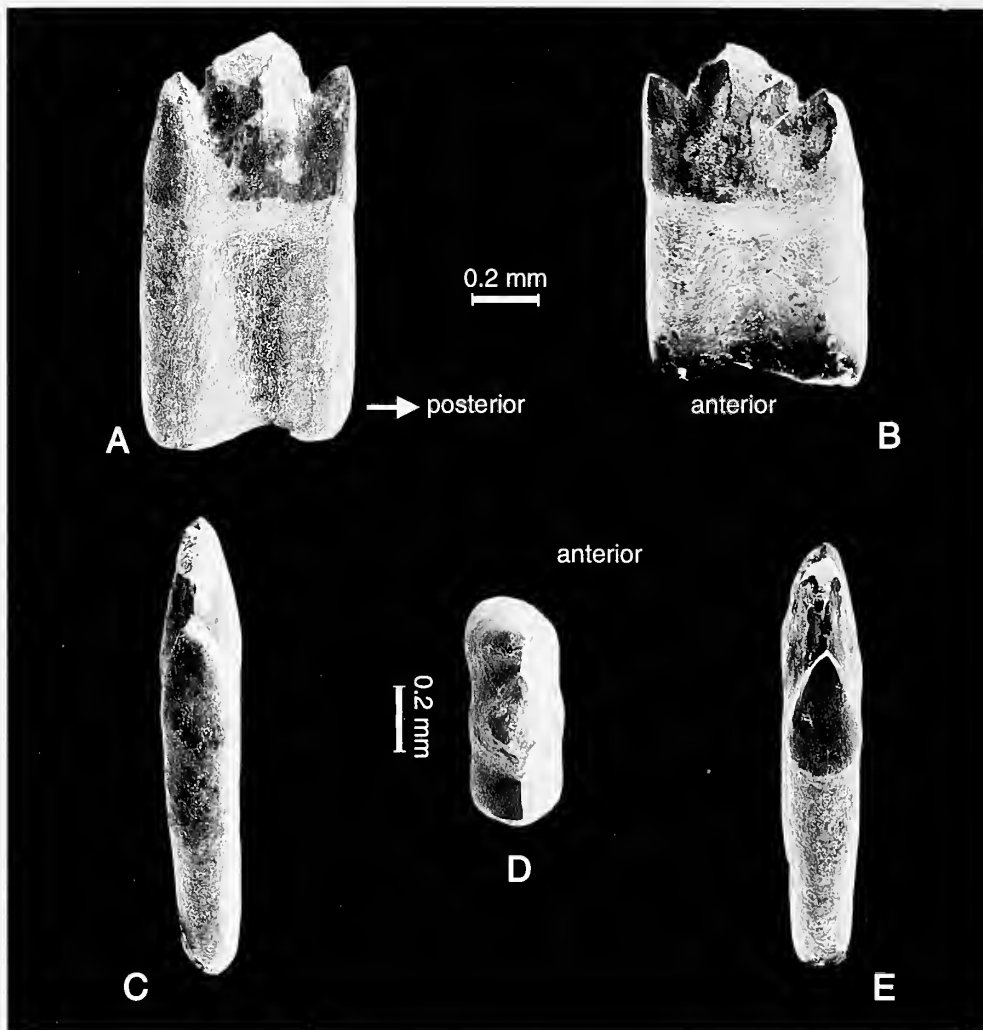


Fig. 6.—*Rewaconodon tikiensis* (GSI Pal/CHQ-004; Dromatheriidae, Cynodontia). Anterior postcanine (orientation uncertain): A, lateral (labial) view. B, medial (lingual) view. C, anterior (?) view. D, crown (occlusal) view. E, posterior (?) view.

1991; Shubin et al., 1991). More recent studies have shown that this feature has a more complex systematic distribution among the groups of advanced cynodonts and early mammaliaforms (e.g., Cui and Sun, 1987; Luo, 1994; Sigogneau-Russell and Hahn, 1994). *Rewaconodon*, *Mitrodon* and *Microconodon*, all of which were recently discovered or restudied, demonstrate that root division and its precursor condition have an even wider systematic distribution than previously thought.

Several cynodonts are known to have a degree of variation of the root division (Luo, 1994; Shapiro and Jenkins, 2001). Incipient division of the root occurs in *Pachygenelus* from North America (Shubin et al., 1991), but it was variable and less developed in the African *Pachygenelus* (Gow, 1980). A derived condition of root division may occur in cynodonts that are otherwise very primitive in crown characters and dental replacement.

Complete root division is present in *Mitrodon*, but this non-mammalian cynodont retains the primitive alternating, multiple and wave-like dental replacement (Shapiro and Jenkins, 2001). Among mammaliaforms, root division of postcanines is variable in different tooth loci in *Sinoconodon* (Luo, 1994), in some molariform teeth of *Kuehneotherium* (Parrington, 1971) and *Morganucodon watsoni* (personal observation). In short, the presence of some degree of root division suggests that dromatheriids (including *Rewaconodon*) are more derived than other cynodonts that lack this feature, such as: thrinaxodontids, probainognathians, chiniquodontids (*sensu stricto*), and gomphodonts (*sensu stricto*). However, presence of root division and its precursor condition, by themselves, are not sufficient to indicate a close mammalian affinity. By the incipient root division, dromatheriids are no more closely related to mammals than either tritylodontids

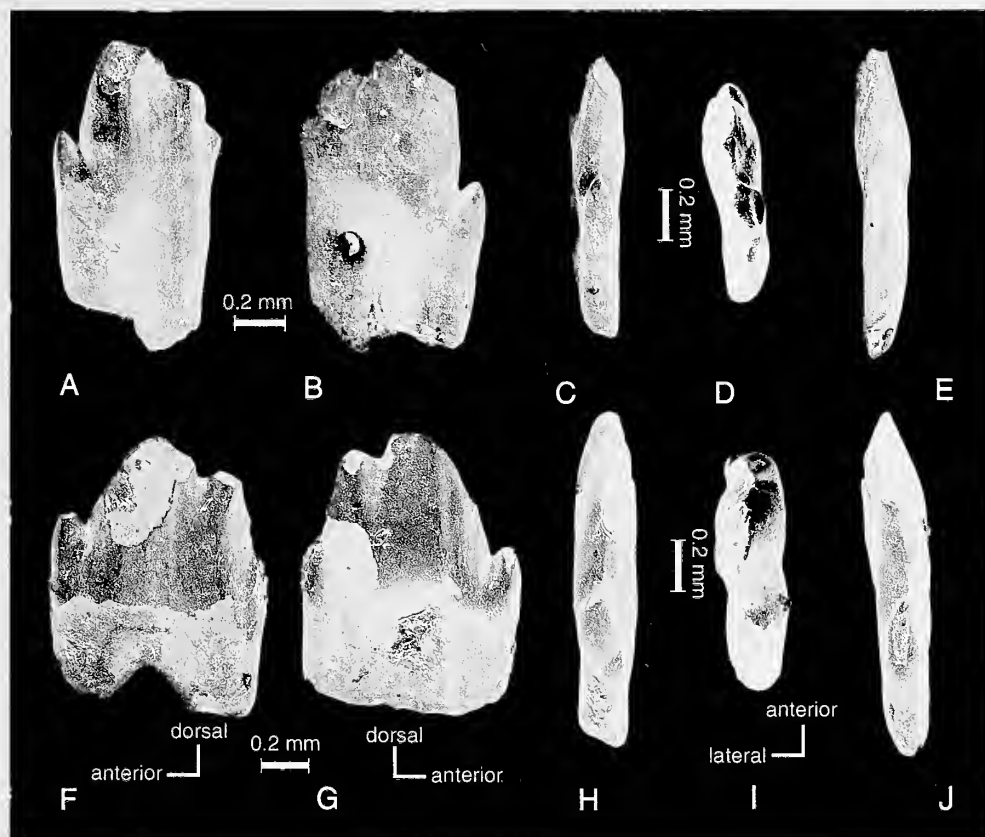


Fig. 7.—*Rewaconodon tikiensis* (Dromatheriidae, Cynodontia): Lower left tetracuspoid postcanines. GSI Pal/CHQ-007: A, lateral (labial) view. B, medial (lingual) view. C, posterior (distal) view. D, crown (occlusal) view. E, anterior (mesial) view. GSI Pal/CHQ-008: F, lateral (labial) view. G, medial (lingual) view. H, anterior (mesial) view. I, crown (occlusal) view. J, posterior (distal) view.

(with full division of multiple roots) and tritheledontids (also with incipient division of roots) (Sues, 2001; Luo et al., 2002).

Although many non-mammalian cynodonts have developed some degree of root division, dromatheriids, *Therioherpeton* and *Pachygelemus* are unique in that the dividing grooves extend for the full length of the root on the lingual and labial sides. This is one of the few derived characters useful for distinguishing them from other derived non-mammalian cynodonts. The postcanine root structure is nearly identical in *Rewaconodon*, *Dromatherium*, *Microconodon* and *Therioherpeton* (Simpson, 1926; Bonaparte and Barberena, 1975, 2001; Sues, 2001). The root structure of the tetracuspoid postcanine of *Rewaconodon* is also similar to that of *Lepagia* but different from (better divided than) that of *Pseudotricodon* (Hahn et al., 1984).

Biogeographic implications.—The newly discovered dromatheriid *Rewaconodon* also has biogeographic implications. Through the transition from the Late Triassic to Early Jurassic, the global terrestrial tetrapod assemblages are dominated by widely spread and

cosmopolitan families, indicating that there were few geographic barriers to the exchanges of terrestrial tetrapods among major landmasses (Shubin and Sues, 1991). The newly recognized dromatheriid *Rewaconodon* in the Tiki Formation of India extends the geographic distribution of dromatheriids, previously known from the Carnian sediments of the Newark Supergroup and the Dockum Group of North America (Sues et al. 1994; Lucas and Oakes, 1988; Sues et al. 1994), and from Norian-Rhaetian sediments of Europe (Hahn et al. 1994; Godefroit, 1997; Godefroit and Battail, 1997; Godefroit et al., 1998). These dromatheriids are possibly closely related to therioherpetids from the Carnian strata of the Santa Maria Formation of Brazil (Hahn et al., 1987, 1994; Battail, 1991; Bonaparte and Barberena, 1975, 2001; Abdala and Ribeiro, 2000). This new evidence corroborates the hypothesis that the faunal transition from the Late Triassic to the Early Jurassic is accompanied by an increasingly cosmopolitan nature of the continental tetrapod assemblages (Shubin and Sues, 1991).

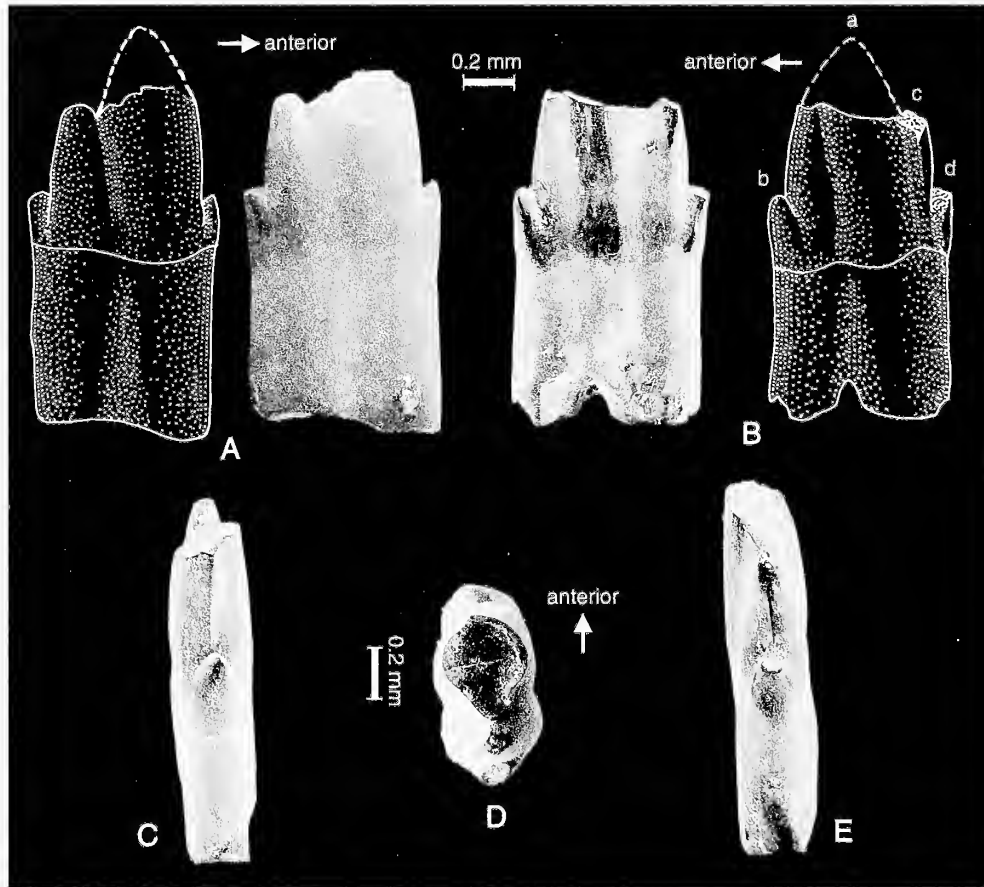


Fig. 8.—*Rewaconodon tikiensis* (GSI Pal/CHQ-006; Dromatheriidae, Cynodontia). A tetracuspid postcanine (tooth locus and orientation uncertain): A, lateral (labial) view. B, medial (lingual) view. C, anterior (?) view. D, crown (occlusal) view. E, posterior (?) view.

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NEW DECAPOD CRUSTACEANS (THALASSINIDEA, GALATHEOIDEA, BRACHYURA) FROM THE MIDDLE OLIGOCENE OF PATAGONIA, ARGENTINA

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ABSTRACT

A robust decapod fauna from middle Oligocene rocks near Bariloche, Argentina, has yielded several new forms. New genera include *Baricarcinus* and new species include *Callianopsis australis*, *Proterocarcinus corsolini*, *Trichopeltarion levis*, *Baricarcinus mariae*, and *Asthenognathus microspinus*. *Munda casadioi* (Schweitzer and Feldmann, 2000a) is also reported. This is the first notice of *Callianopsis* de Saint Laurent, 1973, in the southern hemisphere. The species of *Trichopeltarion* and *Asthenognathus* described herein are the oldest known representatives of their respective genera, and *Asthenognathus* is one of the oldest known genera within the Pinnotheridae de Haan, 1833. The fauna of the Foyel Formation is significantly different from that of the slightly younger Centinela Formation, exposed approximately 500 km to the south, suggesting that paleoecological conditions were conducive to specialization in the decapod fauna of southern South America.

KEY WORDS: Decapoda, Brachyura, Thalassinidea, Galatheaidea, Río Foyel, Patagonia, Oligocene, Argentina

INTRODUCTION

The fossil decapod crustacean fauna known from southern South America is becoming increasingly robust as more and more studies are conducted in the region. Thus far, the work has been concentrated in basins known to have had direct connections with the Atlantic Ocean (Aguirre-Urreta, 1987; Feldmann et al., 1995, 1997; Schweitzer and Feldmann, 2000a, b, c, 2001a). These works have resulted in many new genera, species, and records for fossil decapod crustaceans.

The Río Foyel Formation crops out in the Andes Mountains just south of the resort town of Bariloche,

Argentina (Fig. 1), and its macroinvertebrate fauna has received little treatment to date. The recent activity of collectors in the region near Bariloche, Río Negro Province, Argentina, has resulted in a large collection of fossil decapods and other invertebrates. The new decapods described here provide an important comparison with previous studies because of the possible connection of the basin with both the Atlantic and the Pacific oceans. In fact, the decapods of the Río Foyel Formation, described here, display both Atlantic and Pacific affinities.

GEOLOGIC SETTING

Trans-tensional stress occurring during the Oligocene resulted in a number of basins along the eastern margin of the Andes (Dalla Salda and Franzese, 1987; Ramos, 1999). The best known among them is the Ñirihuau Basin, located to the west of the Northern Patagonian Massif and east of an Oligocene volcanic arc formed

during a period of oblique convergence of the South American and Farallón plates (Spalletti and Dalla Salda, 1996). The Ñirihuau basin is an elongate (200 km) and narrow (20 to 45 km) depression bounded by strike-slip faults. The sedimentary infilling was controlled by contemporaneous tectonic and magmatic activity (Cazau,

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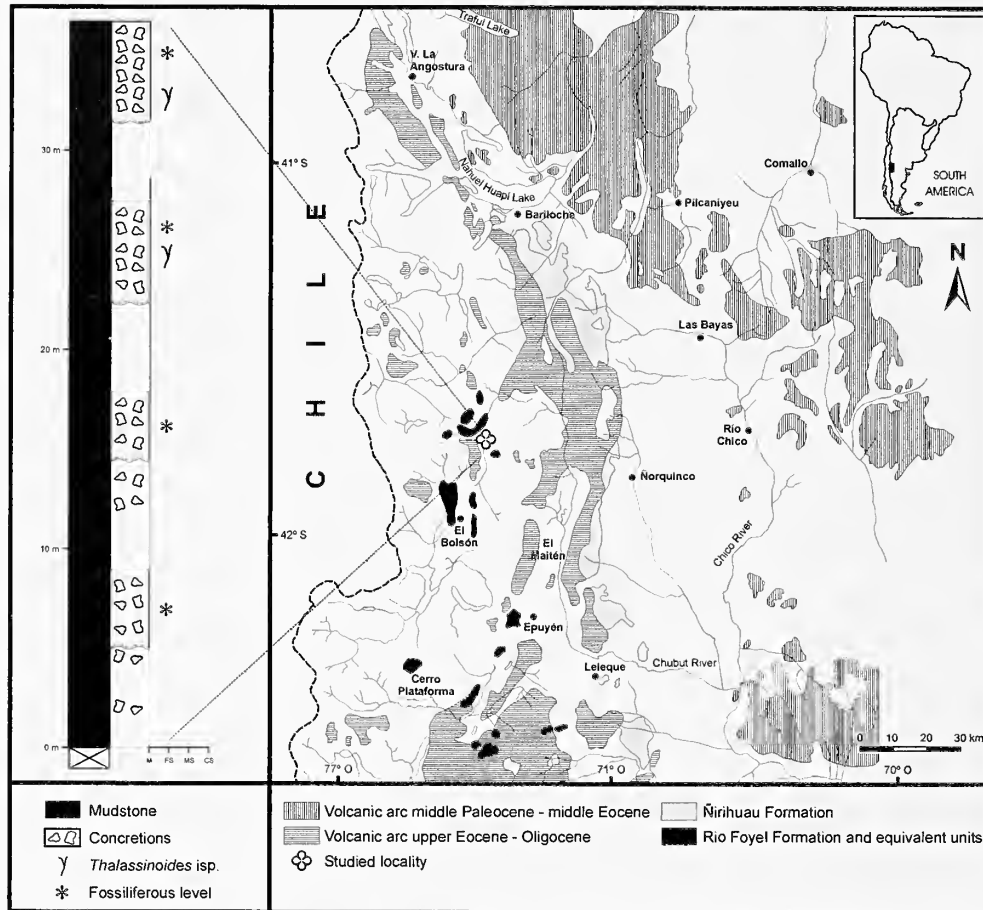


Fig. 1.—Geologic map and stratigraphic section showing the Río Foyel Formation and the position of the locality from which decapods were collected. Map modified from Spalletti and Matheos (1987).

1980; Spalletti, 1983; Franchi et al., 1984). This sedimentary infilling reaches 2,000 to 2,500 m in thickness and includes two stratigraphic units, the Ñirihuau Formation at the base and the overlying Collón Cura Formation (González Bonorino and González Bonorino, 1978; Spalletti, 1981; Cazau et al., 1989). Although both units are predominantly continental, the former includes an Oligocene event of marine sedimentation exposed along the southern coast of Lake Nahuel Huapi.

A smaller contemporaneous basin developed to the southwest, located between the Oligocene volcanic arc and the positive structural elements placed further West and which was a remnant of the Jurassic and Cretaceous volcanic arcs (Spalletti and Matheos, 1987). The sedimentary infilling of this basin includes shallow marginal lake deposits of the Ñirihuau Formation overlying marine rocks referred to the probably equivalent Río Foyel, Las Minas and Rincón de Chollila formations (Diez and Zubia, 1981). The area covered by this basin, as well as its relation to the Ñirihuau Basin, have not been determined with any degree of certainty. The textural and compositional characteristics of the infilling suggest little transport

and quick burial of the sediments in a subsiding basin associated with an undissected magmatic arc (Spalletti and Matheos, 1987). These features suggest that the Oligocene–Miocene rocks deposited to the west of the Ñirihuau Basin represent the infilling of an intra-arc basin.

The decapod crustaceans studied in this paper were collected from rocks referred to the Río Foyel Formation. These rocks are exposed along the left bank of the Foyel River (S 41° 43.589'; W 71° 27.480'), in Río Negro Province (Fig. 1). All of the decapods described herein were collected from these outcrops.

The stratigraphic section considered herein measures 36 m thick, although González Bonorino (1944) estimated that it may reach more than 150 m thick (Fig. 1). The section includes alternate beds of massive shale and concretions with irregular contact surfaces. The shales are up to 5.5 m thick and contain isolated subspherical concretions of different sizes. In some beds they are finely laminated, although the original stratification is probably diagenetically erased. The concretionary beds are up to 5 m thick and yield abundant concretions of different shapes (spherical, ovate and tubular) and sizes (0.5–20 cm

diameter). The concretions contain, in addition to the decapods studied, the coral *Flabellum* sp.; the brachiopod *Terebratella* sp.; the pelecypods *Panopea nucleus* (Ihering), *Dosinia* sp., *Neilo* sp., *Nucula* sp., *Atrina* sp., *Brachidontes* sp., *Zygochlamys* sp., and *Cucullaea* sp.; the gastropods *Turritella* sp. and *Fusinus* sp.; and the echinoderm *Schizaster?* sp., as well as vertebrate remains. Gallery tubes referred to *Thalassinoides* are also present in these beds.

The depositional paleoenvironment of this unit is controversial. Ramos (1982) and Spalletti (1983) stated that it was deposited in an open marine environment. On the other hand, Bertels (1994b) suggested the existence of unstable environmental conditions, which were fluctuating and restricted, with two events of an increase in water depth at the base and top of the sequence separated by deposits generated in very low energy marginal marine environments. Barreda et al. (2003) inferred a restricted littoral marine environment, with temperate to warm, nutrient-rich water of less than normal salinity. The lithology and the presence of concretions suggest an environment of low energy and low sedimentation rate. Fossils within the concretions exhibit fine details of the original structure, suggesting that the concretions may have formed immediately after deposition by primary precipitation by means of diagenetic reactions between sediment that was rich in organic matter and the interstitial water.

The age of the Río Foyel Formation has been the subject of diverse opinions. Bertels (1980, 1993, 1994a, b) assigned it an early middle Oligocene age based upon foraminiferans. Chiesa and Camacho (2001) stated an Eocene age, while Barreda et al. (2003) suggested it was late Oligocene–early Miocene. Pöthe de Baldi (1984) described the pollen content of this unit and recognized

two assemblages. The first one contains *Notofagidites* and low percentages of *Podocarpites*. The second assemblage yielded a low percentage of *Notofagidites*, a high frequency of trilete spores, and a significant percentage of saccate gymnosperms in which the outstanding element is *Phyllocladites mawsonii*. This would suggest an age closer to the early middle Oligocene age proposed by Bertels (1994a), as there are no modern herbaceous and arbustive elements. According to Guerstein et al. (in press), these elements are present in the Centinela Formation, indicating a modernization of the flora beginning near the Oligocene–Miocene boundary.

Ramos (1982) related the marine deposits of the Río Foyel Formation to a Pacific transgression. However, analysis of the molluscan fauna from Río Foyel, Cerro Plataforma and the valley of Epuyén support closer relationships with the Oligocene–Miocene sequence exposed along the Atlantic coast of Patagonia (Feruglio, 1949; Griffin et al., 2002). Likewise, Bertels (1980) stated that the foraminiferan assemblage from the Río Foyel Formation is the same one, albeit impoverished, found in sediments of the Atlantic Austral basin during the Oligocene–Miocene time. Thus, the paleontological evidence suggests that during Oligocene–Miocene, this basin had a strong connection with the Atlantic Ocean and perhaps a more restricted connection with the Pacific Ocean.

REPOSITORIES FOR TYPE AND STUDIED MATERIAL

CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

GHUNLPam: Departamento de Ciencias Naturales, Geological Museum, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina.

MSNM: Museo Civico di Storia Naturale di Milano, Milano, Italy.

SYSTEMATIC PALEONTOLOGY

- Infraorder Anomura MacLeay, 1838
- Superfamily Galatheoidea Samouelle, 1819
- Family Galatheididae Samouelle, 1819
- Subfamily Galatheinae Samouelle, 1819
- Genus *Munida* Leach, 1820

Austromunida Schweitzer and Feldmann, 2000a, p. 151, fig. 3, 4.

Type Species.—*Pagurus rugosus* Fabricius, 1775.

Discussion.—Schweitzer and Feldmann (2000a) described the new genus *Austromunida* with *A. casadioi* Schweitzer and Feldmann, 2000a, based upon three more or less complete specimens (holotype GHUNLPam 16832; paratypes GHUNLPam 16833, 16834) from the middle Eocene Centinela Formation on Estancia 25 de Mayo, Calafate, Santa Cruz (Argentina), now considered to be late Oligocene–early Miocene. Even though the authors pointed out a superficial similarity with *Munida* Leach, 1820, they justified the institution of the new genus on morphological characters not present in other

known fossil galatheids, such as the narrow, needle-like rostrum; and numerous lateral spines. However, the recent discovery of a rich sample of galatheids from Bariloche has called into question the systematic validity of *Austromunida* Schweitzer and Feldmann, 2000a. Garassino and De Angeli (2003) have synonymized *Austromunida* with *Munida*; justifications therein will not be repeated here.

Munida casadioi (Schweitzer and Feldmann, 2000a)
(Fig. 2, 3)

Diagnosis.—Carapace subrectangular, longer than wide; central rostral spine long, needle-like; supraocular spines short, needle-like; lateral margin slightly convex, with one strong antero-lateral spine; one strong hepatic spine; three strong epibranchial spines; two strong mesobranchial spines; one strong posterior branchial spine; cervical and branchiocardiac grooves deep;

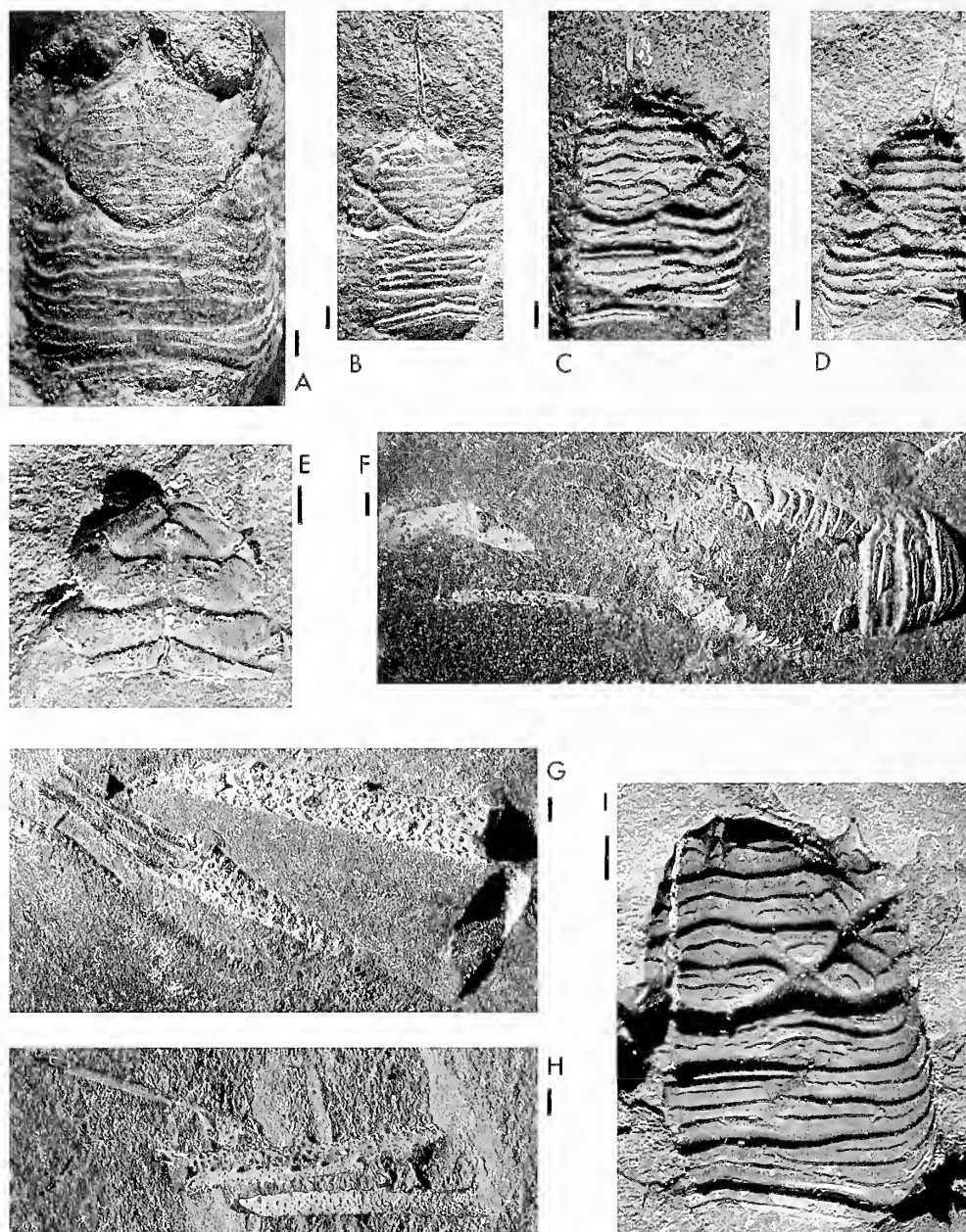


Fig. 2.—*Munida casadioti* (Schweitzer and Feldmann, 2000a). A. MSNM i26085, complete carapace with long central rostral spine, needle-like and two well-developed supraocular spines, needle-like; B. MSNM i25745, complete carapace with long central rostral spine, needle-like; C. MSNM i26087, complete carapace with long central rostral spine, needle-like and one well-developed supraocular spine, needle-like; D. MSNM i25700, complete carapace with long central rostral spine, needle-like and one well-developed supraocular spine, needle-like; E. MSNM i25799, thoracic sternites subtriangular, with arcuate striae; F. MSNM i26073, complete specimen with well-preserved abdominal somites; G. MSNM i25735, pereopods 1; H. MSNM i26088, pereopods 1; I. MSNM i25750, incomplete carapace with well-developed antero-lateral spine. Scale bars equal to 1 mm.

carapace ornamented by continuous striae and four pairs of epigastric spines, linearly arranged transversely; subtriangular thoracic sternites; pereopod 1 very elongate; abdominal somite 2 with six small spines; abdominal somite 3 with four small spines on dorsal surface.

Material Examined.—We ascribe to this species 164 specimens from the Bariloche area, so divided: 134 fragmentary and complete carapaces, MSNM i23031 a–b, i25627, i25629, i25630–i25649, i25651–i25658,

i25660, i25661, i25663, i25665–i25693, i25695–i25715, i25736–i25740, i25742–i25756, i25894, i26065–i26067, i26069–i26077, i26079–i26087, i26089–i26091, and GHUNLPam 25.034–25.038; 7 specimens composed of abdominal somites (MSNM i23027, i25662, i25664, i25799, i26078, i26088); 23 specimens composed of thoracic appendages (MSNM i23019, i23020, i25716–i25720, i25722–i25735, i25741, i25880, i25881, i26088).

Measurements.—Maximum length of the carapace ranges between 0.7 and 1.5 cm.

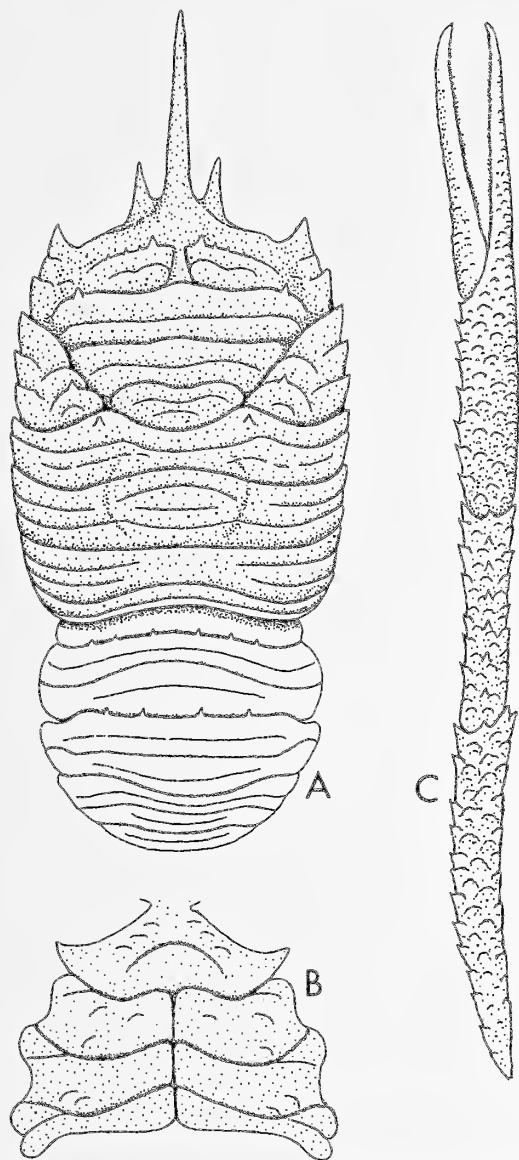


Fig. 3.—*Munida casadioi* (Schweitzer and Feldmann, 2000a). A. Reconstruction of carapace and abdomen; B. Subtriangular thoracic sternites with arcuate striae; C. Pereiopod 1.

Description.—Carapace, excluding rostrum, slightly longer than wide, subrectangular in dorsal view, slightly convex in transverse section and flattened in longitudinal section, with regions crossed by thin, transverse, serrated striae. Frontal margin slightly oblique. Central rostral spine long, needle-like. Orbits with concave upper orbital margin and with weak supraocular relief. Supraocular spines short, slightly convergent and directed upwards. Lateral margins of carapace long, weakly convex, with seven strong spines directed forward: one spine located in anterior anterolateral angle, one spine on hepatic margin, three on epibranchial margin, two on mesobranchial margin. Cervical and branchiocardiac grooves well developed, deep. Four pairs of epigastric spines linearly arranged transversely, median pair stronger than others. Anterior mesogastric process marked by weak groove. Small hepatic regions with small spine. Epibranchial regions marked by cervical and branchiocardiac grooves, subtriangular, with three short, sinuous striae and with one spine. Posterior regions marked by three main continuous transverse striae and more or less discontinuous minor striae.

Mesobranchial spine close to branchiocardiac groove. Cardiac region bounded on margins by weak depression. Thoracic sternites subtriangular, with arcuate striae. Second to fourth abdominal somites with four transverse striae. Abdominal somite 2 with six small submedian spines on anterior ridge. Abdominal somite 3 with four small submedian spines on anterior ridge. Pereiopod 1 chelate, very elongate. Subcylindrical merus, carpus and propodus with spines and with small, sinuous striae. Occlusal margins of dactylus and fixed finger finely serrulate.

Discussion.—Schweitzer and Feldmann (2000a) pointed out the main characters of *Munida*: carapace rectangular or ovoid, longer than wide; rostral spine flanked by one pair of supraorbital spines; two or three anterolateral spines; several small, lateral spines posterior to intersection of cervical groove with lateral margin; deep, arcuate cervical groove; transverse carapace ridges that range from simple and parallel to complex and bifurcating; and a linear array of gastric spines paralleling frontal margin of carapace. The main characters of *Munida* can be found in the study specimens.

This genus is known in the fossil record from four species, distributed from the Danian (Lower Paleocene) to Miocene: *Munida primaeva* (Seegerberg, 1900) from the Danian of Denmark; *M. quadrolonga* Schweitzer and Feldmann, 2000a, from the Eocene of Washington, USA; *M. konara* Schweitzer and Feldmann, 2000a, from the Oligocene–Miocene of Alaska; and the middle Oligocene to Miocene *M. casadioi*. Two indeterminate species are also known from the Miocene of Japan (Seegerberg, 1900; Takeda et al., 1986; Collins and Jakobsen, 1994; Jakobsen and Collins, 1997; Schweitzer and Feldmann, 2000a; Kato, 2001).

Collins and Jakobsen (1994, tab. 10, fig. 2) and Jakobsen and Collins (1997, tab. 2, fig. 8) reported the presence of *Munida primaeva* in the decapod fauna from the Danian of Denmark, without giving its morphological description. The poor state of preservation of the lectotype of this species, lacking the rostral spine and the supraorbital and anterolateral spines, makes comparison with *M. casadioi* (Schweitzer and Feldmann, 2000a) difficult. However, the presence of two epigastric spines, one spine on the epibranchial region, and one spine on the posterior branchial region distinguish *M. casadioi* from the Danish species.

Munida quadrolonga was described on two more or less complete specimens (Schweitzer and Feldmann, 2000a, p. 154, fig. 6). *Munida casadioi* differs from this species because *M. casadioi* has only one anterolateral spine, only two epigastric spines, one spine in the hepatic region and one spine on hepatic margin, three spines along the epibranchial margin and two on the mesobranchial margin. *Munida konara* was described based upon five very incomplete specimens (Schweitzer and Feldmann, 2000a, p. 156, fig. 7). Even though the comparison between *M. casadioi* and *M. konara* is difficult because of the poor state of preservation of the latter species, the presence of only one anterolateral spine distinguishes *M. konara* from *M. casadioi*. In addition, the carapace of *M. konara* is broader than *M. casadioi*.

Infraorder Thalassinidea Latreille, 1831

Superfamily Callianassoidea Dana, 1852

Family Ctenochelidae Manning and Felder, 1991

Genus *Callianopsis* de Saint Laurent, 1973

Included Species.—*Callianopsis australis* new species; *C. callamensis* (Withers, 1924); *C. goniophthalma* (Rathbun, 1902) (recent only); *C. muratai* (Nagao, 1932) (= *Callianassa elongatodigitata* Nagao, 1941; *Callianassa kusiroensis* Nagao, 1941); *C. titaensis* (Nagao, 1941); *Callianopsis* spp. Kato, 1996; ?*C. inornatus* Schweitzer and Feldmann, 2001b. Unless otherwise marked, all are exclusively fossil.

Diagnosis.—Carapace with dorsal oval and cardiac prominence; low rostral carina, rostral spine; sixth abdominal somite with lateral projections; uropod lacking notch or incision; major cheliped with proximal meral hook and keel; carpus of major cheliped with flange extending from lower margin. Manus of male rectangular, with large tubercles on outer surface; distal margin with spine at midheight; fixed finger with spine or prominence at midlength; movable finger usually with large nodes and keel on outer surface. Manus of female narrow, gracile, with smaller tubercles on outer surface; movable finger with small nodes and less robust keel. Minor chela smaller and more slender than major chela (after Manning and Felder, 1991; Schweitzer-Hopkins and Feldmann, 1997).

Discussion.—Although only one extant species of *Callianopsis* is known, there are several fossil species. The morphology of the major cheliped is remarkably consistent throughout the genus, with species being differentiated primarily by the ornament on the manus and the shape of the merus. *Callianopsis* is notable in displaying very distinct sexual dimorphism, recognizable in fossil and extant species (Schweitzer-Hopkins and Feldmann, 1997).

The new material exhibits nearly all of the generic level diagnostic features of the major chela; the carapace is unavailable for study. The only generic features that are missing in the new material concern the ornamentation on the fixed finger and the swelling along the distal margin of the manus. However, these regions of the new fossil material are crushed or broken; thus, it is not possible to observe them. The manus of the minor chela is somewhat more stout than in other species of the genus, but it is still much smaller than the major chela. Thus, the new material is confidently referred to *Callianopsis*.

The discovery of a species of *Callianopsis* in the southern hemisphere represents a major range extension. Other fossil species of *Callianopsis* are known only from the North Pacific realm, while the sole extant species ranges from coastal Alaska to Baja California. The oldest known species is possibly *Callianopsis? inornatus* from Eocene rocks of the Olympic Peninsula, Washington (Schweitzer and Feldmann, 2001b), and the oldest species known with certainty are those named by Nagao (1941) from the Eocene of Japan. The extension of the

geographic range to the middle Oligocene of Patagonia suggests that the genus had an amphitropical distribution by the late Oligocene. The genus appears to have originated in the North Pacific Ocean during the Eocene and subsequently dispersed to the high southern latitudes, perhaps by moving into deeper, colder water to cross the equatorial region. The extant species, *C. goniophthalma*, is known from deep-water localities and is restricted to west coastal North America, which is bathed by cool-water currents from the North (Schweitzer-Hopkins and Feldmann, 1997). It appears to be quite possible that the distribution of the genus is controlled by temperature factors as well as depth preferences, because all fossil species are known from moderate to high latitudes and the extant species is known from deep, cool water areas.

Callianopsis australis, new species

(Fig. 4)

Types.—Holotype, GHUNLPam 25.000 and 2 paratypes, GHUNLPam 25.001 and 25.002; paratypes MSNM i25608, i25613–i25616, i25626; CM 52515, cast of MSNM i25626; CM 52516, cast of MSNM i25608; CM 52522, cast of GHUNLPam 25.000.

Diagnosis.—Merus of major cheliped stout, with very small spine on proximal lower margin; manus of major cheliped of male with large tubercles distally, distal margin with blunt spine above position of fixed finger; fixed finger of male chela curving upward, with long, blunt projection on occlusal surface; manus of minor chela stout for genus.

Etymology.—The trivial name is the Latin word *australis*, meaning southern, in reference to this species of the genus being the first known from the Southern Hemisphere.

Description.—Ischium of major cheliped longer than high, highest distally and narrowing proximally; upper margin convex distally and becoming concave proximally; distal margin sinuous, convex at upper margin at articulation with carpus, concave at lower margin; lower margin weakly concave; remainder of article unknown.

Merus of major cheliped not much longer than high, L/H about 1.6, bulbous; with blunt, longitudinal keel dividing merus longitudinally into two portions, upper portion much larger; proximal margin nearly straight; lower margin with very small spine at proximal corner, spine directed downward, remainder of margin convex; distal margin angular, facilitating articulation with carpus; upper margin markedly convex.

Carpus of major cheliped higher than long, L/H about 63 percent, proximal margin with long projection at upper corner at articulation with merus, remainder convex, merging with lower margin; lower margin bounds a flange extending downward from main portion of article; upper margin weakly convex; distal margin weakly concave.

Manus of male major cheliped longer than high, H/L averaging about 92 percent, rectangular, ornamented with large tubercles distally, moderately vaulted longitudinally especially distally, moderately vaulted transversely especially along upper margin; proximal margin with small projection at upper corner at articulation with carpus, with small notch under projection, remainder of margin nearly straight; upper margin nearly straight; lower margin proximally weakly convex, becoming concave just proximal to fixed finger; distal margin straight at upper portion, becoming sinuous with blunt spine just above position of fixed finger; inner surface smooth, weakly convex centrally.

Fixed finger curving upward, with long, blunt projection on occlusal surface, shorter and narrower than movable finger. Movable finger stout,

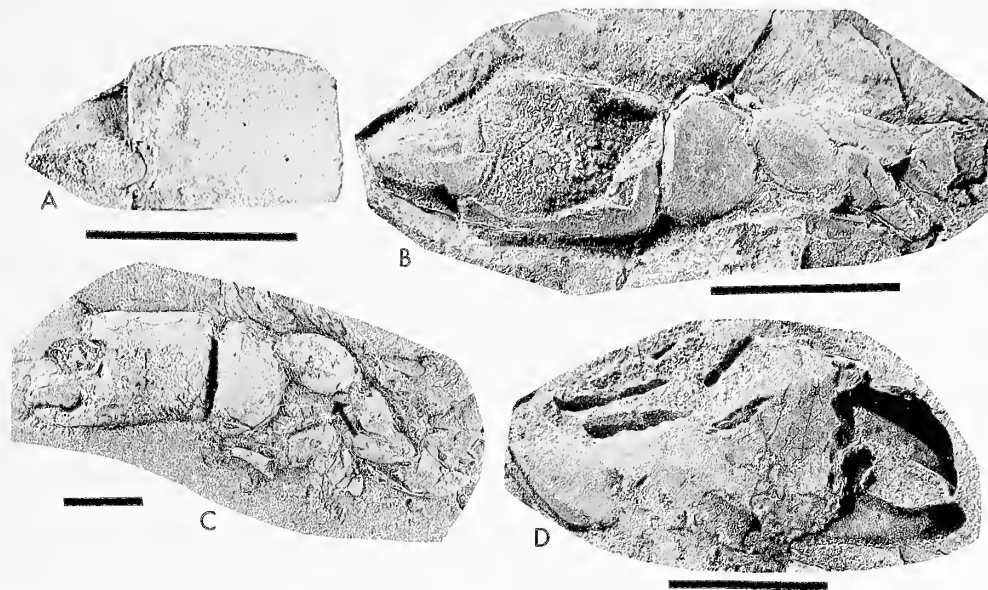


Fig. 4.—*Callianopsis australis* new species. A. Exaflex© cast of manus of major chela, paratype MSNM i25608 (counterpart), showing granular ornamentation; B. Major cheliped, paratype MSNM i25608 (part); C. Major cheliped, and portion of minor cheliped, holotype GHUNLPam 25.000, arrow indicates tiny spine on merus diagnostic for genus; D. Portion of manus and fingers of major chela, showing granular ornamentation on lower margins of manus and fixed finger, paratype MSNM i25616. Scale bars equal to 1 cm.

narrowing distally, weakly arched; with blunt tooth proximally, possibly articulating with blunt spine on distal margin, to be used for crushing.

Manus of minor chela of similar shape to major chela but much smaller.

Remainder of appendages and carapace unknown.

Measurements.—Measurements (in mm) taken on articles of the major cheliped of specimens of *Callianopsis australis*: GHUNLPam 25.000: maximum length of manus (L1), 15.2; maximum height of manus (H1), 13.0; length of fixed finger (L2), >6.6; length of movable finger (L3), >11.3; maximum height of carpus (H2), 13.0; maximum length of carpus (L4), 6.9; maximum length of merus (L5), 9.7; maximum height of merus (H3), 7.2; MSNM i25608: L1, 10.0; H1, 9.0; L5, 9.7; H3, 7.2; GHUNLPam 25.001: L1, 15.7; H1, 14.9; MSNM i25626: L1, 7.4; H1, 7.0; L3, 4.3; H2, 6.0; L4, 6.9; L5, 5.0; H3, 2.9.

Discussion.—*Callianopsis australis* is represented by one very well preserved specimen, retaining the manus, carpus, merus, and ischium, and four rather poorly preserved specimens. However, each has contributed to the description of the species. The meral hook, while tiny (Fig. 4C), is clearly exhibited on the holotype, GHUNLPam 25.000. The movable finger of GHUNLPam 25.001 exhibits a tiny portion of keel proximally, but the remainder is crushed.

Callianopsis australis can be differentiated from other species by its blunt projection on the fixed finger; all other species have a spine in that position. The merus is more stout in *Callianopsis australis* than in the other species of the genus, and the minor chela is more stout in *C. australis* than in other species, in which it is slender and gracile.

The specimens of *Callianopsis australis* all appear to be males because they exhibit the rectangular manus and heavy ornamentation typical of males of *Callianopsis* (Schweitzer-Hopkins and Feldmann, 1997). However, the specimens range considerably in size, and the two smaller specimens may be juveniles, which have less differentiated chelae and are thus of indeterminate gender in fossils (Schweitzer-Hopkins and Feldmann, 1997).

Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polybiinae Ortmann, 1893

Genus *Proterocarcinus* Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995

Type Species.—*Proterocarcinus lophos* Feldmann, Casadío, Chirino-Gálvez, and Aguirre, Urreta, 1995, by monotypy.

Other Species.—*Proterocarcinus latus* (Glaessner, 1933), as *Archaeogeryon*; *Proterocarcinus corsolini* n. sp. herein.

Diagnosis.—Carapace transversely ovoid to hexagonal, wider than long, 0.60–0.76 times as long as wide; front narrow, downturned, with four spines including inner-orbital spines; orbits extremely broad, rimmed, fronto-orbital width to width ratio 0.70–0.95, two orbital fissures; anterolateral margin short, with four spines including outer-orbital spines; epibranchial ridge elevated, granular, terminating at base of fourth anterolateral spine; branchial region swollen, with longitudinal ridge

parallel to long axis of cardiac region; first pereopods isochelous; propodus and dactylus of fifth pereopod paddle-like (Schweitzer and Feldmann, 2000b, p. 644).

Discussion.—The genus was originally described based upon specimens collected from Danian rocks of the Roca Formation in the Neuquén Basin, Río Negro Province, Argentina and subsequently was identified in the upper Oligocene–lower Miocene Centinela Formation in Santa Cruz Province. Thus, it is possible that the genus spans much of the Cenozoic.

Although identification of species referable to *Proterocarcinus* based upon the diagnostic characters is straightforward, there is the potential for confusion based upon the discovery that juvenile specimens of *Chaceon peruvianus* (d'Orbigny, 1842) bear a strong resemblance to adult *Proterocarcinus latus* (Glaessner, 1933) (Schweitzer and Feldmann, 2000b). Details of surface morphology and ornamentation are strikingly similar although the width of the fronto-orbital margin is very great in juvenile and adult *Proterocarcinus* (FOW/W = 0.84–0.91) whereas that margin is somewhat narrower in juvenile *Chaceon* Manning and Holthuis, 1989 (FOW/W = 0.80–0.82) and much narrower (FOW/W = 0.52–0.63) in adults. Additionally, the anterolateral margin of *Chaceon* bears five spines, and there are fewer than five in *Proterocarcinus*.

The problem of distinguishing between species of the two genera has been made more confusing by the addition of the generic name, *Lebucarcinus* Bahamonde and Frassinetti, 1980, that may be a synonym of *Chaceon*. Bahamonde and Frassinetti (1980) proposed this name in recognition that a species named *Cancer tyro* by Philippi (1887) was not a member of *Cancer*. Unfortunately, the holotype of *Cancer tyro* illustrated by Philippi (1887, pl. 50, fig. 3) apparently no longer exists. Bahamonde and Frassinetti (1980) noted that it had been in the collection of Francisco J. Ovalle, but they did not indicate that they had confirmed that the type was missing. Chirino-Gálvez (1993), citing Porter (1910), concluded that the specimen was probably lost in the earthquake and fire of 1906 in Chile. The type is not in the collections of the Museo Nacional de Historia Natural, Santiago, where many of Philippi's types are deposited. As a result, Bahamonde and Frassinetti (1980, p. 276) designated SGO.PI.3422 in the Museo Nacional de Historia Natural, Santiago, as the neotype of *Cancer tyro*. The neotype bears no resemblance to the illustration of the type specimen of *Cancer tyro* nor does it fit the type description. Furthermore, the neotype was collected at Punta de Fraile, some 65 km north from the type locality at Lebu. Thus, the validity of the type designation, and therefore the validity of the name *Lebucarcinus* is called into question (International Code of Zoological Nomenclature, 1999, Article 75).

The original description of *Cancer tyro* is: "Cephalothorax subhexagonal, wider than long, moderately convex above, granulo-squamose on protuberances, depressed

parts very smooth; front margin entirely semi-orbicular, lateral margin entirely straight, posterior margin somewhat arcuate, extended, half the breadth of cephalothorax flattened, front weakly downturned, tridentate, teeth very short, truncated." (Philippi, 1887, p. 214, translated from Latin by the authors) The Spanish elaboration on the description is: "A wide transverse depression, almost horizontal, extends behind the orbits from one side to the other; the margin of the carapace, which corresponds to this depression, is broken. The genital and cardiac regions are almost exactly the same size and same form and terminate on each side in a point; the former is extended toward front in a well-marked beak. The form of these regions is almost as that observed in the genus *Pseudocarcinus* [error pro *Pseudocarcinus*] [H.] Milne Edwards. Both regions are granulose, another similarity is the three lateral protuberances which lie on either side. The extremity of the left hand is preserved, the fingers are very slender and the index is very flattened and armed with very fine, closely spaced teeth." (Philippi, 1887, p. 214, translated from Spanish by the authors)

Examination of the single illustration of the specimen referred to *Cancer tyro* by Philippi (1887) shows that the specimen had a length/width ratio of 0.86, a frontal width/width ratio of 0.23, a fronto-orbital width/width ratio of 0.46, and a posterior width/width ratio of 0.4. These values fall within or are close to the ratios taken from adult specimens of *Chaceon peruvianus* (Schweitzer and Feldmann, 2000b). Furthermore, the anterolateral margin, although broken, seems to be quite irregular as though it bore several spines.

By contrast, the description of *Cancer tyro* given by Bahamonde and Frassinetti (1980), based upon the neotype and one additional specimen referred to the species, SGO.PI.3443, is: "Cephalothorax subpentagonal, densely granulated, slightly convex, rather flattened, with anterolateral margin containing two large, subequal spines located in its posterior half. Base of anterior spine a little wider than base of posterior spine, both have smooth borders. Posterolateral margins nearly straight, very gently curved.

"Orbits are rather wide, well defined, with a thick raised margin, with external corner not dentiform, smooth without spines or prominent granules. Front narrow, slightly inclined downwards, smoothly trilobed; the metagastric and cardiac lobes identifiable. Posterior margin of the carapace smooth with well pronounced border, finely granulated.

"Chelipeds well developed, large, but not strong; right a little more developed than left, with the propodus a bit shorter. Propodus slightly scaly, provided externally with three carinae, one large, another medium and very noticeable, and one small; the uppermost parts are the most scaly. Fingers are thin, with fine closely spaced teeth, black in color.

"The ambulatory legs are finely and uniformly granulated, with the merus smooth, relatively wide and

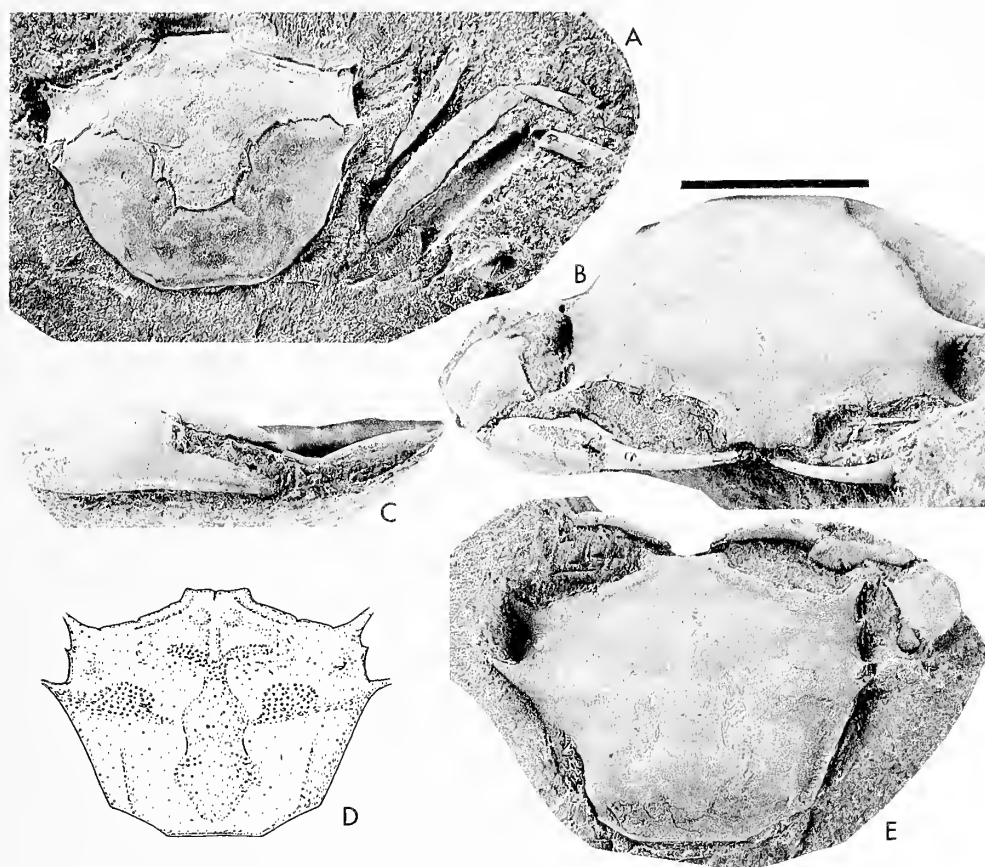


Fig. 5.—*Proterocarcinus corsolini* new species. A. Dorsal carapace and appendages, paratype MSNM i25803a; B. Oblique anterior view of dorsal carapace, showing orbits and rostrum, holotype GHUNLPam 25.010; C. Cheliped of holotype, GHUNLPam 25.010; D. Composite line drawing of dorsal carapace; E. Dorsal carapace of holotype, GHUNLPam 25.010. Scale bar equal to 1 cm.

flattened. Only the first four pairs of legs can be seen while the fifth one is not visible. No significant remains of the abdomen have been found.

“The stridulating apparatus is clearly defined.” (Bahamonde and Frassinetti, 1980, p. 276, translated from Spanish by Luis Chirino-Gálvez)

The dimensions taken from the neotype of *Cancer tyro*, SGO.PI.3422, are almost precisely those of *Proterocarcinus latus* (Schweitzer and Feldmann, 2000b); frontal width/width = 0.17; fronto-orbital width/width = 0.87; posterior width/width = 0.30, and length/width = 0.76. The orbital margin is very long, straight, and sloping posteriorly. The anterolateral margin bears two large spines; if other, intermediate spines exist, they are not visible on the low resolution photographs. These are all characteristics of *P. latus*.

Accordingly, we therefore conclude that the neotype designated by Bahamonde and Frassinetti (1980) for *Cancer tyro* should be rejected on the grounds that they published the neotype and the new generic name solely for that purpose (ICZN, 1999, Article 75.2), they did not adequately document the loss of the holotype (ICZN, 1999, Article 75.3.4), the description and illustrations of the neotype do not conform to the sense of the original

designation both in terms of the description and the illustration by Philippi (1887) (ICZN, 1999, Article 75.3.5), and the neotype was not collected near the type locality (ICZN, 1999, 75.3.6). Further, we conclude that the original description of *Cancer tyro* (Philippi, 1887) lies within the boundaries of *Chaceon*.

The specimen designated as the neotype of *Cancer tyro* and, therefore, the type species of *Lebucarcinus*, most closely conforms to the sense of *Proterocarcinus*. Thus, we place the specimens studied by Bahamonde and Frassinetti into *Proterocarcinus*. Finally, following the rules of nomenclature, the removal of the type species from *Lebucarcinus* renders the generic name a *nomen nudum*.

Proterocarcinus corsolini, new species (Fig. 5)

Types.—Holotype, GHUNLPam 25.005, and paratypes GHUNLPam 25.006–25.033; paratypes MSNM i23005, i23030, i25802, i25803, i25822; possibly chela GHUNLPam 25.074; paratypes CM 52505–52507; CM 52517, cast of MSNM i25803; CM 52518, cast of MSNM i25822; CM 52524, cast of GHUNLPam 25.074.

Table 1.—Measurements (in mm) taken on the dorsal carapace of specimens of *Proterocarcinus corsolini*. L = maximum carapace length; W = maximum carapace width; FW = frontal width; FOW = fronto-orbital width; PW = posterior width.

Specimen	L	W	FW	FOW	PW
GHUNLPam 25.010 Holotype	16.1	18.5	4.7	16.7	6.1
GHUNLPam 25.011	11.9	14.2	—	12.1	4.8
MSNM i125803a	16.2	19.8	4.6	17.1	7
GHUNLPam 25.012	19.8	23.8	6.4	—	8.9
CM 52505	~10.6	11.8	—	10.6	4.2
MSNM i125581	16.6	20.2	4.8	16.2	6
GHUNLPam 25.029	18.4	22.2	6.4	21.4	7.1
CM 52506	ca. 16.6	20.1	—	19.2	7.5
GHUNLPam 25.007	11.7	13.1	2.8	12	4.3
MSNM i123005	11.4	13	2.8	11.5	4.9
GHUNLPam 25.013	~27	~29.4	7.4	26.4	—

Diagnosis.—*Proterocarcinus* with moderately broad frontal margin bearing four broadly rounded teeth; long orbital margins that slope posterolaterally; three anterolateral teeth, the medial one of which is greatly reduced; and moderately well-defined carapace regions with distinct longitudinal ridge on metabranchial region.

Etymology.—The trivial name recognizes the contribution of Rodolfo Corsolini, Museo del Lago Gutiérrez "Dr. Rosendo Pascual" in Bariloche, Río Negro, Argentina, who collected much of the material described in this study and who assisted the authors in the field.

Description.—Moderate sized for genus. Carapace generally quadrate in outline, longer than wide; weakly arched transversely, more strongly vaulted longitudinally; regions weakly defined as elevated areas.

Front broad, 24 percent maximum width, excluding spines, more or less straight, downturned, with two blunt inner orbital projections and bilobed axial projection. Orbits very broad, well-defined orbital rim becoming obscure laterally; fronto-orbital width about 88 percent maximum width, straight, sloping posterolaterally to terminate in anterolaterally projecting anterolateral spines; two small orbital notches, one at midlength and one near base of outer orbital spine. Anterolateral margin shorter than posterolateral margin, straight, nearly parallel long axis, with three anterolaterally directed spines including outer orbital spine; medial spine small or reduced to node. Posterolateral margins straight, well defined, converging posteriorly. Posterior corners truncated as long, straight elements bounding moderately wide, straight posterior margin, about 32 percent maximum width.

Regions of carapace defined as broad, slightly swollen areas with granular surfaces separated by broad, shallow depressed areas. Frontal region extends to level of medial orbital fissures, well defined as swollen areas flanking shallow, axial sulcus. Hepatic regions weakly defined, bearing centrally located node at level of second anterolateral spine. Protogastric regions large, weakly elevated to form transverse ridge with granular surfaces, separated by long, narrow mesogastric region, broadening slightly posteriorly to level of last anterolateral spine then widening abruptly to merge with metagastric region which bears pair of small pits and is flanked by well defined arcuate grooves. Cardiac region very broad; with subtle transverse ridge, weakly depressed axially; narrowing posteriorly into indistinct intestinal region. Mesobranchial region with broad, distinct ridge extending from metabranchial region to last anterolateral spine. Metabranchial region with narrow, distinct longitudinal ridge defining steeply sloping lateral portion of metabranchial region and terminating just inside posterolateral corner.

Abdomen and venter not known.

First pereopods isochelous. Carpus nearly equidimensional when viewed from above, strongly inflated, keel defines outer margin. Keel extending transversely parallel to distal margin, with prominent spine on inner distal corner. Propodus longer than high, maximum height at distal

end of hand, keeled on upper surface; broad ridge extends from lower articulation with carpus to base of articulation with dactylus. Lower margin weakly concave, keeled to tip of fixed finger. Length of fixed finger about equal to length of hand. Dactylus smooth; upper surface curved downward toward tip; curved slightly toward posterior when viewed from above. Denticles of occlusal surfaces poorly preserved, appear to be moderately large, blunt spines with darkened tips.

Measurements.—Measurements, in millimeters, taken on specimens of *Proterocarcinus corsolini* are given in Table 1.

Discussion.—The description of *Proterocarcinus corsolini* brings to three the number of species referred to *Proterocarcinus*. As discussed above, it is probable that some Chilean specimens, previously referred to the genus *Lebucarcinus* should be assigned to *Proterocarcinus*; however, that decision must await examination of the specimens in question. In addition, Aguirre Urreta (1987) referred specimens from Península Valdés, Chubut Province, Argentina, to *Lebucarcinus tyro*. In all likelihood, this material, which is currently being restudied, is referable to *Proterocarcinus*.

Proterocarcinus corsolini shares generic characteristics with the two previously described species; but, it can readily be distinguished from them. Although the front is not known from the type species, *P. lophos*, the anterolateral margin exhibits four prominent spines and the dorsal surface has subdued topography and lacks clear longitudinal ridges on the metabranchial regions. By contrast, *P. corsolini* has three anterolateral spines, the medial one being reduced; the regions are more distinctly defined; and a prominent longitudinal ridge extends across the metabranchial region. *Proterocarcinus latus* exhibits a dorsal surface that is reminiscent of *P. corsolini*, but the former species has four anterolateral spines, the medial two of which are reduced; the orbital margin does not slope posterolaterally to the same extent that it does in *P. corsolini*; and the rostrum is more projected and bears more prominent teeth. The ratio of frontal width to total width is 17 percent in *P. latus* and 24 percent in *P. corsolini*.

Superfamily Cancroidea Latreille, 1802

Family Atelecyclidae Ortmann, 1893

Genus *Trichopeltarion* A. Milne Edwards, 1880

Trichopeltarion A. Milne Edwards, 1880:19.

Trachycarcinus Faxon, 1893:156.

Type Species.—*Trichopeltarion nobile* A. Milne Edwards, 1880, p. 20, pl. 2.

Included Species.—See Schweitzer and Salva (2000) and Salva and Feldmann (2001).

Diagnosis.—A recent diagnosis of the genus was given by Salva and Feldmann (2001) and will not be repeated here.

Discussion.—*Trichopeltarion* and related genera have recently been studied in depth (Schweitzer and Salva, 2000; Salva and Feldmann, 2001) so that a re-examination of the details of definition of the genus is not

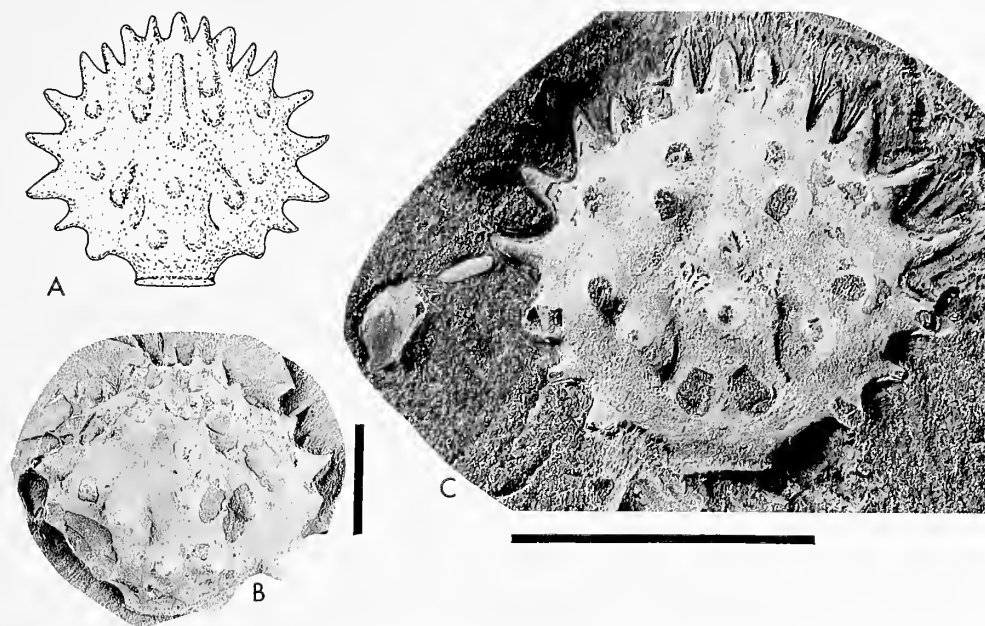


Fig. 6.—*Trichopeltarion levis* new species. A. Composite line drawing of dorsal carapace; B. Dorsal carapace, holotype GHUNLPam 25.040; C. Dorsal carapace, paratype MSNM i25533. Scale bars equal to 1 cm.

necessary herein. The specimens from the Bariloche region conform to the generic diagnosis of the carapace in all regards so that placement within the genus is certain. The carapace is nearly circular, the rostrum is not strongly produced and is trifid, the upper orbital margin bears three spines separated by deep clefts, the lateral margins exhibit simple spines, and the regions tend to be swollen, separated by broad, shallow grooves, and with discrete spines.

Trichopeltarion has the most robust fossil record of any member of the Atelecyclidae. The new species described here is the oldest known species of the genus. *Trichopeltarion berglundorum*, from late Oligocene to early Miocene age rocks in Washington state (Schweitzer and Feldmann, 1999), is the second oldest species of the genus. Thus, this suggests that the genus arose in the southern hemisphere with subsequent dispersal to the northern hemisphere and also westward into the western Pacific and Indian oceans (Table 3). *Levicyclus* Schweitzer et al., 2002, is known from Eocene rocks of Baja California Sur, México, which marks the earliest known occurrence of the family. *Atelecyclus* Leach, 1814, has been reported from Miocene to Pleistocene occurrences in North Africa and Europe (Glaessner, 1969), but these occurrences have yet to be verified.

Trichopeltarion levis, new species
(Fig. 6)

Types.—Holotype GHUNLPam 25.040, paratypes GHUNLPam 25.039, 25.041, 25.042; paratypes, i23026, i25524a and b, i25528a and b, i25533a and b; paratypes CM 52500–52504; CM 52514, cast of MSNM i25533; CM52523, cast of GHUNLPam 25.039.

Diagnosis.—Carapace ornamented only by very fine pustules; frontal, orbital, and lateral spines simple; posterolateral spines well developed; carapace regions bearing 14 prominent, simple spines.

Etymology.—The trivial name is from the Latin *levis*, meaning smooth, referring to the generally smooth carapace surface.

Description.—Carapace small for genus, circular, transversely and longitudinally vaulted; bearing simple spines on front and lateral margins and prominent, sharply-pointed spines on dorsal surface.

Front trifid, not extended significantly beyond margin, with elongated spines of equal length with rounded terminations; median spine broader than lateral ones. Orbits directed weakly anterolaterally, defined by three spines; inner orbital spine approximately equilateral; medial and outer orbital spines more slender; outer orbital spine curved anteriorly. Two anterolateral spines, slender, simple, curved slightly anteriorly. Three posterolateral spines, decreasing in length posteriorly; anteriormost stout, equilateral; medial spine narrow, elongate; posteriormost spine defined as blunt protuberance. Posterior margin sharply defined, produced posteriorly, with prominent, thickened, pustulose rim.

Regions of carapace defined by subtle, broad depressions. Mesogastric region elongate, slender anteriorly, broadening posteriorly and bearing prominent spine near posterior margin. Protogastric regions elongate, narrow, extending from outer frontal spine weakly posterolaterally; bearing two spines arrayed on either side of midline of carapace, anteriormost spine smaller than prominent, domal posterior one. Metagastric region nearly circular, with strong axial spine. Urogastric region not differentiated. Cardiac region defined laterally by deep, arcuate branchiocardiac grooves and bearing pair of prominent spines arrayed transversely. Intestinal region depressed with subtle axial swelling. Hepatic region a weak swelling with centrally located spine. Gastric regions not well differentiated, bearing two prominent spines set equidistant from posterolateral margin. Surface of carapace ornamented by extremely fine pustules.

Remainder of organism not preserved.

Measurements.—Measurements, in mm, taken on the dorsal carapace are given in Table 2. Measurements of total length and width were made exclusive of the spines.

Table 2.—Measurements (in mm) taken on specimens of *Trichopeltarion levis* new species. L = total carapace length; WT = total carapace width; WR = rostral width; WP = posterior width.

Specimen number	L	WT	WR	WP
MSNM i25533	12.8	12	3	4.9
MSNM i25524	21.2	20.9	3.9	11.4
MSNM i25528	Broken	Broken	Broken	Broken
GHUNLPam 25.041	9.7	ca. 8.8	2.3	4.3
CM 52504	Broken	25.7	5.7	Broken
GHUNLPam 25.039	17.9	16.3	3.7	9.8
GHUNLPam 25.040 Holotype	20.8	21.7	4	10.9
GHUNLPam 25.042	18.9	18.7	3.6	9.2

Discussion.—Species of *Trichopeltarion* are distinguished from one another on the basis of the carapace outline; the degree to which carapace regions are distinctly delimited by grooves; the nature of ornamentation of the carapace, exclusive of spines and nodes; and the form and development of spines on the margins and on the surface of the carapace (Table 3). Although *Trichopeltarion levis* bears all the characters allying it with the genus, its morphology is clearly different from all previously known species. Thus, its identity as a new species is certain. The plexus of characters; circular outline, 19 simple marginal spines including the rostral and orbital spines, smooth carapace surface separating smooth tubercles, and only moderately-defined regions, is exhibited by no other described species. The most similar form is *T. merrinae* Schweitzer and Salva, 2000, from the late Miocene of New Zealand; however, *T. merrinae* has an elongate carapace with both simple and complex marginal spines and a granular carapace surface between granular tubercles. Both species have a large number of marginal spines compared to other species of the genus, including three pairs on the posterolateral margin.

Superfamily Xanthoidea MacLeay, 1838
Family Pilumnidae Samouelle, 1819

Discussion.—Several advances have recently been made in assigning fossil genera to the Pilumnidae, a family which has historically been largely overlooked by paleontologists who have favored placement of taxa in the Xanthidae *sensu lato* MacLeay, 1838 (Glaessner, 1969). Schweitzer (2000) placed several genera into the Pilumnidae *sensu lato* with no attempt at placing them into subfamilies; those genera included *Actinmnus* Dana, 1851; *Galene* de Haan, 1833; *Galenopsis* A. Milne Edwards, 1865; *Glabropilumnus* Balss, 1932; *Lobogalenopsis* Müller and Collins, 1991; *Pilumnominus* Müller and Collins, 1991; *Pilumnopus* A. Milne Edwards, 1863; *Pilumnus* Leach, 1815; and *Pulalus* Schweitzer et al., 2000. Davie (2002) has provided useful diagnoses for extant members of the family and several of the constituent subfamilies.

Schweitzer (2000) discussed the Pilumnidae in the fossil record and suggested methods by which to assign

fossils to the family. The most prominent characters that are preservable in the fossil record that can be used to assign some genera to the family are the pronounced longitudinal vaulting of the carapace in the anterior third; long protogastric and hepatic regions; carapace width not much greater than length; medially notched front; poorly defined regions; anterolateral margin being shorter than posterolateral margin; arcuate epibranchial regions; and possession of 2–4 small, usually blunt, anterolateral spines.

These characters best fit the Galeninae Alcock, 1898, and the Pilumninae Samouelle, 1819, as defined by Davie (2002). As stated by Schweitzer (2000, p. 736), “this combination of characters is diagnostic only for some pilumnids. Therefore, the diagnosis should allow some fossil specimens to be assigned to the Pilumnidae, although it will not be diagnostic for all members of the family.” In fact, the Halimedinae Alcock, 1898; Rhizopinae Stimpson, 1858; Calmaniinae Števčić, 1991, and Eumedoninae Dana, 1853, diverge markedly from this diagnosis (Davie, 2002). The Galeninae possess very poorly developed regions and lack acute spines on the anterolateral margins. Members of the Pilumninae usually have well-defined regions and have acute spines on the anterolateral margins (Davie, 2002).

The Galeninae embraces only one extant genus, *Galene* (Davie, 2002), which has an Indo-Pacific distribution and is also known in the fossil record from Pliocene and Pleistocene rocks of that region (Glaessner, 1969). The Miocene *Galene proavita* Glaessner, 1960, has recently been moved to *Carcinoplax*, a decision with which we concur (Karasawa and Kato, 2003a). *Pulalus* and *Tumidocarcinus* are quite similar to extant *Galene* in many regards; Schweitzer (2000, p. 736) discussed the remarkable similarity between Eocene and Oligocene *Pulalus* and the extant *Galene*. Species of *Tumidocarcinus* are also quite similar to *Galene* in possessing a four-lobed front, sub-equal anterolateral and posterolateral margins or anterolateral margins somewhat longer than the posterolateral margins, weakly developed carapace regions, a strongly vaulted carapace, and a similar shape and arrangement of carapace regions. *Paratumidocarcinus* appears to be quite similar in shape and ornamentation to *Tumidocarcinus*, based upon the illustration and brief description (Martins-Neto, 2001). *Baricarcinus* new genus is herein allied with these genera due to its possession of a highly longitudinally vaulted carapace, weakly defined regions, blunt protuberances on the anterolateral margins, long protogastric and hepatic regions, and anterolateral margins shorter than posterolateral margins. Thus, it appears that these fossil species are best allied with *Galene*; however, work in progress by one us (CS) is addressing that issue.

Aguirre-Urreta et al. (1995) named a new species of *Tumidocarcinus*, *T. forsteri*. It does not belong to the genus for several reasons. Species of *Tumidocarcinus* are extremely large and inflated; *T. forsteri* exhibits neither

Table 3.—Species of *Trichopeltarion* and features of the dorsal carapace of each. SPINE = nature of the ornament of individual spines; SURF = ornamentation of dorsal carapace surface; REG = definition of dorsal carapace regions; TUBS = nature of carapace tubercles; # = number of anterolateral spines; S = smooth; G = granular; R = reduced.

Species	Age	Outline	Spine	SURF	REG	TUBS	#
<i>T. nobili</i> A. Milne Edwards, 1880	Recent	Circular	Complex	G	Moderate	G	15
<i>T. alcocki</i> (Doflein, 1903)	Recent	Elongate	Simple	G	Distinct	G	15
<i>T. balssi</i> (Rathbun, 1932)	Recent	Circular	Complex	G	Distinct	G	13?
<i>T. berghmdorum</i> Schweitzer and Feldmann, 1999	l. Olig.-early Miocene	Elongate	Simple	S	Distinct	G	15
<i>T. corallinus</i> (Faxon, 1893)	Recent	Elongate	Simple	S	Indistinct	G	15
<i>T. crosneri</i> (Guinot, 1986)	Recent	Elongate	Complex	G	Distinct	G	15
<i>T. decorns</i> (Rathbun, 1945)	Miocene	Circular	Simple	G	Moderate	?	?
<i>T. elegans</i> (Guinot and Sakai, 1970)	Recent	Circular	Simple	G	Indistinct	G	13
<i>T. fantasticum</i> Richardson and Dell, 1964	Recent	Elongate	Complex	G	Moderate	G	15
<i>T. glaucus</i> (Alcock and Anderson, 1899)	Recent	Elongate	Complex	G	Distinct	G	15
<i>T. granulosa</i> (Schweitzer and Salva, 2000)	Miocene	Elongate	Simple	G	Distinct	S	15
<i>T. greggi</i> Dell, 1969	l. Mio.	Circular	Complex	G	Indistinct	R	15
<i>T. luziokai</i> (Imazumi, 1951)	Miocene	Circular	Complex	G	Distinct	S	15
<i>T. inflatus</i> (Kato, 1996)	Miocene	Circular	Simple	S	Distinct	G	13
<i>T. intesi</i> (Crosnier, 1981)	Recent	Elongate	Complex	G	Moderate	G	13
<i>T. merrinae</i> Schweitzer and Salva, 2000	late Miocene	Elongate	Both	G	Moderate	G	19
<i>T. moosai</i> (Guinot, 1989)	Recent	Elongate	Simple	G	Moderate	G	15
<i>T. ovalis</i> (Anderson, 1896)	Recent	Circular	Simple	G	Moderate	G	15
<i>T. sagamiensis</i> (Rathbun, 1932)	Recent	Elongate	Complex	G	Distinct	G	19
<i>T. spinulifer</i> (Rathbun, 1898)	Recent	Elongate	Complex	G	Moderate	G	17
<i>T. wardi</i> Dell, 1968	Recent	Elongate	Complex	G	Distinct	G	15
<i>T. levis</i> new species	Eocene	Circular	Simple	S	Moderate	S	19

feature. Carapace regions are moderately well defined in *T. forsteri*, and the carapace is flattened, neither of which are possessed by any other species of *Tumidocarcinus*. The orbits of *T. forsteri* are small and narrowly spaced, while those in other *Tumidocarcinus* are larger and more broadly spaced. The front is quadrilobed in *Tumidocarcinus*, while in *T. forsteri*, it is axially sulcate and appears to be triangular and downturned. The carapace of *T. forsteri* is flattened, lacking the pronounced vaulting of the carapace typical of *Tumidocarcinus* and other members of the subfamily. Thus, it should be removed from *Tumidocarcinus*. However, placement of this species into a genus and family must await examination of the type specimens.

Alphonse Milne Edwards (1865, p. 316) considered *Galenopsis* to be quite similar to *Galene* (= *Galena* in his work) in its smooth carapace, quadri-lobed front, short anterolateral margins as compared to the posterolateral margins, and blunt spines or protuberances on the anterolateral margins. Schweitzer (2000) concurred as did Karasawa and Kato (2003a). However, *Galenopsis* cannot be placed within the Pilumnidae, because the abdomen of males extends beyond the anterior edge of the chelipeds (see A. Milne Edwards, 1865, pl. 8, fig. 2a), which is not characteristic of the Pilumnidae. In addition, the anterolateral margins of *Galenopsis* are much shorter than those of most Pilumnidae, and the carapace is much more flattened than in most authentic pilumnids.

Galenopsis appears to be best placed within the Goneplacidae MacLeay, 1838, as suggested by Glaessner (1969), based upon its flattened, rectangular carapace; poorly defined regions; broad fronto-orbital width; short

anterolateral margins with small, sharp spines; notched, straight front; and free male abdominal somites. The subfamily Euryplacinae Stimpson, 1871, accommodates *Galenopsis* well. That subfamily is characterized by poorly defined carapace regions; a straight front with a median notch; broad fronto-orbital width; a distinct supraorbital angle; a short anterolateral margin with 2–5 spines; broadened sternum and a sterno-abdominal cavity reaching the anterior edge of sternite 4; all male abdominal somites free and somites 4–6 much narrower than 3, a telson longer than wide; and an abdomen typically triangular in shape (Davie, 2002; Karasawa and Kato, 2003a). The preserved features of species of *Galenopsis* exhibit features of the subfamily; thus, the genus is placed into the subfamily with confidence. *Galenopsis* is known from Eocene to Oligocene rocks of Europe, east Africa, and India and questionably from Pliocene rocks of Fiji (Glaessner, 1969); these occurrences do not expand the geologic or geographic range of the subfamily as defined by Karasawa and Kato (2003a).

Karasawa and Kato (2003a) performed a phylogenetic analysis on fossil and selected extant members of the Goneplacidae, and they reevaluated those genera previously referred to the Goneplacidae, placing some into the Pilumnidae. In so doing, they assigned *Maingrapsus* Tessier et al., 1999, and *Paracoralliocarcinus* Tessier et al., 1999, to the Pilumnidae, allied with *Georgeoplax* Türkay, 1983. Karasawa and Kato (2003b) indicated that *Georgeoplax* does not have an auxiliary plate on sternite 8, suggesting that it does not belong within in the Chasmocarcininae Serène, 1964. However, Davie (2002) has placed *Georgeoplax* in the Chasmocarcininae of the

Goneplacidae; thus, more work will need to be done to resolve the placement of *Georgeoplax*, *Maingrapsus* and *Paracorallicarcinus*. Members of the Chasmocarcininae possess an auxiliary plate on sternite 8; if that feature were to be assessed in specimens of *Maingrapsus* and *Paracorallicarcinus*, it would help to resolve the problem.

Genus *Baricarcinus*, new genus

Included Species.—*Baricarcinus mariae* new species, by monotypy.

Diagnosis.—as for species.

Etymology.—The genus name is taken from the Greek *karkinos*, meaning crab, and Bariloche, Río Negro Province, Argentina, a resort town and the largest town near the type locality of the new genus in Patagonia, Argentina.

Description.—as for species.

Occurrence.—*Baricarcinus* is known only from the occurrence reported herein.

Discussion.—*Baricarcinus* is represented by two specimens which are moderately well preserved. While they superficially resemble many members of the Pilumnidae and the Xanthoidea, their morphology cannot be embraced by any existing genus. The new specimens are quite similar to species of *Tumidocarcinus*; however, in *Tumidocarcinus*, the carapace is extremely inflated overall; the front is distinctly quadrilobed; the anterolateral margins and posterolateral margins are subequal; and the fronto-orbital width occupies about 50 percent the maximum carapace width. In the new material, the carapace is not greatly inflated overall; the front is bilobed; the anterolateral margin is markedly shorter than the posterolateral margins; and the fronto-orbital width occupies about 65 percent the maximum carapace width. Members of *Galene* have acute spines on the anterolateral margins, while the new material has very weak blunt protuberances. In species of *Galene*, the fronto-orbital width occupies 40 percent the maximum carapace width, while in the new material, the fronto-orbital width is 65 percent the maximum carapace width. The frontal width in species of *Galene* is much narrower than that of the new material, 20 and 37 percent respectively. The new material is easily distinguished from *Pulalins*, in which the carapace regions are moderately well marked, the orbits are fissured, the front is distinctly quadri-lobed, and the fronto-orbital width is much narrower. The new material has none of those attributes. Thus, the new material is placed within a new genus.

Baricarcinus mariae, new species (Fig. 7A–B, D–E)

Types.—Holotype, GHUNLPam 25.003; paratype, GHUNLPam 25.004; CM.52525, cast of GHUNLPam 25.003.

Diagnosis.—Carapace not much wider than long, L/W about 0.85, widest at position of last anterolateral protuberance; regions not well-defined; strongly vaulted

longitudinally, especially in anterior third; front smoothly bilobed; orbits circular, entire, fronto-orbital width about 65 percent maximum carapace width; anterolateral margin shorter than posterolateral, with three blunt protuberances, third largest; epibranchial regions arcuate, with medial swelling and swelling paralleling margin of mesogastric region.

Etymology.—The trivial name honors Dr. Maria B. Aguirre-Urreta, Universidad de Buenos Aires, in recognition of her work on southern hemisphere decapods.

Description.—Carapace not much wider than long, L/W about 0.85, widest at position of last anterolateral protuberance, at about 60 percent distance posteriorly on carapace; regions not well defined; surface appearing to have been weakly granular before weathering; moderately vaulted transversely, strongly vaulted longitudinally, especially in anterior third.

Front about 37 percent maximum width, with smooth notch at midline, lateral edges bordering orbits rounded, produced well in advance of orbits, directed downward. Fronto-orbital width about 65 percent maximum carapace width; orbits circular, directed anterolaterally, entire, upper margin weakly rimmed, outer-orbital angle sharp but not produced. Anterolateral margin convex; shorter than posterolateral margin. measured between outer-orbital angle and last anterolateral protuberance about 45 percent maximum length; initially straight; straight segment followed by two blunt, weak protuberances and third, better developed, protuberance at anterolateral corner. Posterolateral margin weakly convex, entire, weak reentrant at posterolateral corner; length measured between last anterolateral protuberance and posterolateral reentrant about 60 percent maximum carapace width. Posterior margin nearly straight, rimmed, about half maximum carapace width.

Epigastric regions very weakly developed, slightly elevated above remainder of carapace; protogastric regions long, weakly inflated posteriorly; mesogastric region with long, slender anterior process, widening posteriorly, very poorly marked posteriorly; urogastric region depressed, not well-differentiated; cardiac region inflated, especially transversely across midlength of region, hexagonal in shape; intestinal region not well defined.

Hepatic region long, weakly expressed; epibranchial region arcuate, extending from base of last anterolateral protuberance to lateral margins of mesogastric region, with medial swelling; oblong swelling directed obliquely, parallel and adjacent to margin of mesogastric region; remainder of branchial regions undifferentiated, with weak swelling positioned adjacent to midlength of posterolateral margin.

Remainder of carapace and appendages unknown.

Measurements.—Measurements (in mm) were taken on the dorsal carapace of GHUNLPam 25.003 and 25.004 respectively of *Baricarcinus mariae*. Maximum width: 12.2, 11.0; maximum length: 10.4, 9.5; fronto-orbital width, 7.8, 7.2; frontal width, 4.8, 3.9; posterior width, 5.6, 5.2; length to position of maximum width, 6.0, 5.4; length of anterior margin measured between outer-orbital angle and last anterolateral protuberance: 4.9, 4.0; posterolateral width measured between last anterolateral protuberance and posterolateral reentrant: 6.7, 5.2.

Discussion.—The carapace of the new species is much smaller than is typical for other forms that appear to be closely related. However, all other aspects conform well to the diagnosis for the family. Only two specimens are known, suggesting either that the species was relatively uncommon compared to the other taxa reported herein or that it inhabited a niche or exhibited a lifestyle that reduced its possibility of being fossilized.

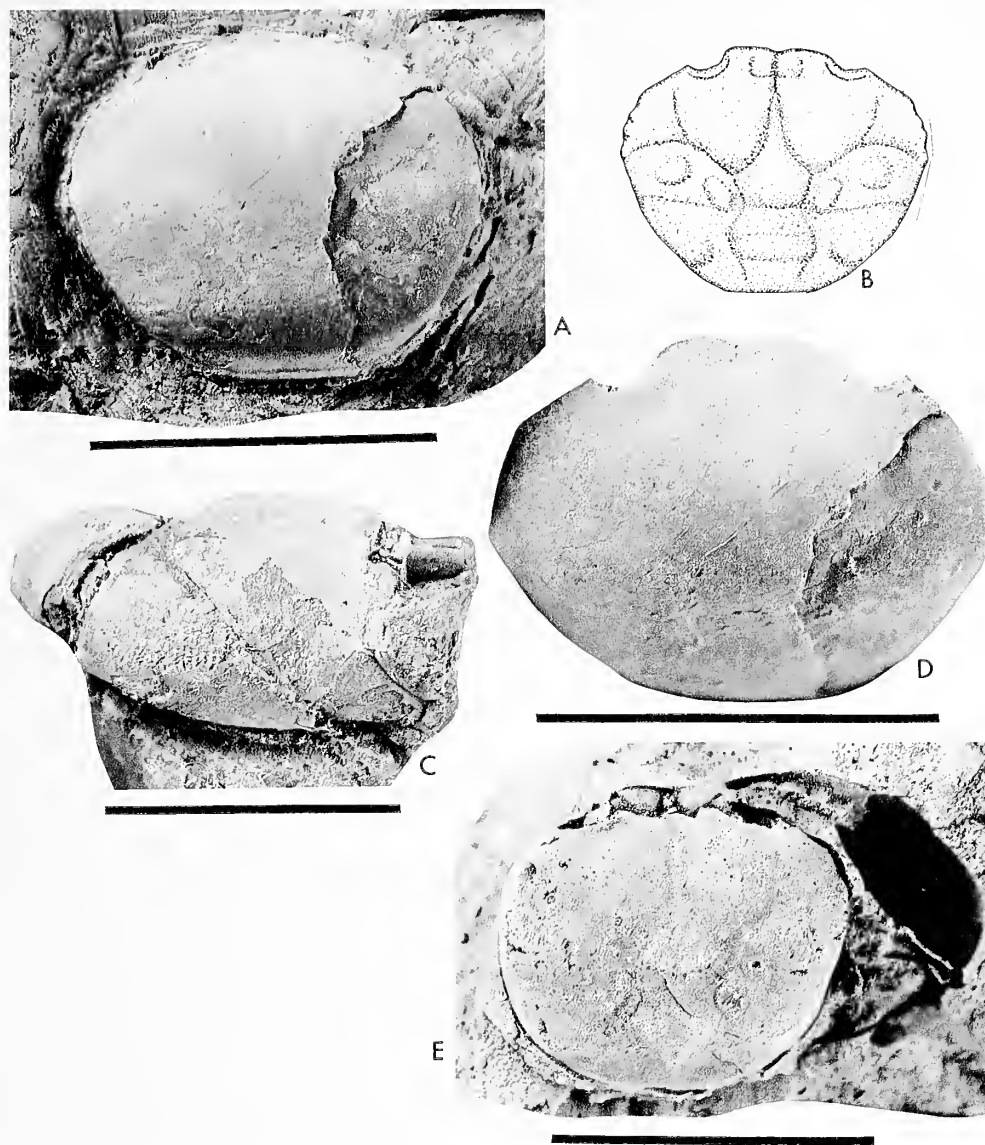


Fig. 7.—Xanthoidea. A. Dorsal carapace of *Baricarcinus mariae* new genus and species, holotype GHUNLPam 25.003; B. Composite line drawing of *Baricarcinus mariae*; C. Indeterminate xanthoid chela, MSNM i23017; D. *Baricarcinus mariae*, oblique anterior view of dorsal carapace, showing front and orbits, holotype GHUNLPam 25.003; E. Dorsal carapace of *Baricarcinus mariae*, paratype GHUNLPam 25.004. Scale bars equal to 1 cm.

Superfamily Pinnotheroidea de Haan, 1833

Family Pinnotheridae de Haan, 1833

Subfamily Asthenognathinae Stimpson, 1858

Included Genera.—*Asthenognathus* Stimpson, 1858;
Tritodynamia Ortmann, 1894.

Diagnosis.—Carapace trapezoidal, wider than long, average length/width about 0.70, typically with a range of 0.54–0.87, typically no higher than 0.79; lateral margins usually steep; regions usually not well-defined; front narrowing distally, deflexed, axially sulcate, usually bilobed, not extending or only slightly extending beyond orbits; orbits shallow; anterior margin usually entirely occupied by orbits, fronto-orbital width to width ratio usually about 0.50, ranging from 0.37–0.70 but typically

no higher than 0.59; anterolateral and posterolateral margins confluent; posterolateral reentrant large; posterior width about half maximum carapace width, ranging from 0.44–0.64; fronto-orbital width to posterior width ratio usually about 1.00, with outliers at about 0.80; branchial region often with inflated epibranchial ridge; sternite 4 without anterior projections (after Schweitzer and Feldmann, 2001a).

Discussion.—Alcock (1900) suggested an arrangement of several subfamilies within the Pinnotheridae including the Asthenognathinae Stimpson, 1858. Pohle and Marques (1998) performed a phylogenetic analysis on the Pinnotheridae, based primarily upon gill structure, and rejected most of these subfamily groupings, including the

Asthenognathinae. In their analysis, *Asthenognathus* formed a monophyletic group of its own (Pohle and Marques, 1998). However, because strong morphological evidence suggests that at least *Asthenognathus* and *Tritodynamia* are closely related (Schweitzer and Feldmann, 1999), we maintain those two genera within the subfamily. Števcíć (1996) had previously suggested the removal of *Mortensenella* Rathbun, 1909, and *Hapalonyx* de Man, 1879, from the Asthenognathinae. Other genera included in the subfamily by Schweitzer and Feldmann (2001a) were not found to be closely related to *Asthenognathus* (Pohle and Marques, 1998) and will need to be evaluated independently, which is beyond the scope of this paper. Interestingly, Pohle and Marques (1998) found *Asthenognathus* to be one of the basal-most, or least derived, groups within the Pinnotheridae, which is supported by its antiquity. *Asthenognathus* is one of the oldest known pinnotherid genera in the fossil record, with Oligocene records in Washington, USA (Schweitzer and Feldmann, 1999) and the new occurrence herein. Other, older pinnotherid occurrences include *Viapinnixa* Schweitzer and Feldmann, 2001a, from the Danian of Greenland (Collins and Rasmussen, 1992) and the Eocene of Mexico (Vega et al., 2001). The Eocene occurrence of *Pinnixa* White, 1846, reported by Glaessner (1969) has since been referred to the Hexapodidae (Schweitzer et al., 2000).

The subfamily diagnosis herein is based upon *Asthenognathus* and *Tritodynamia*, which are very similar in terms of dorsal carapace characters (Schweitzer and Feldmann, 1999). Features of the new species described here, *Asthenognathus microspinosus*, as well as *A. urretae* Schweitzer and Feldmann, 2001a, expand the definition of the genus, and thus the subfamily, as defined by Schweitzer and Feldmann (2001a). Schweitzer and Feldmann (2001a) diagnosed the subfamily as being characterized by a length/width (L/W) ratio of about 0.69, ranging from 0.54–0.79, and *Asthenognathus* as having a L/W of about 0.66. The new species falls outside the range of both the subfamily and the genus, with a L/W of about 0.87 on average. Extant species of *Asthenognathus* have a fronto-orbital width to width ratio of 0.55, as does the new species, while two other fossil members, *A. cornishorum* Schweitzer and Feldmann, 1999, and *A. urretae*, have ratios that are much higher, 0.70. Thus, the range of the fronto-orbital width to width ratio in both the subfamily and the genus is expanded as well.

Genus *Asthenognathus* Stimpson, 1858

Type Species.—*Asthenognathus inaequipes* Stimpson, 1858, by original designation.

Included Species.—*Asthenognathus atlanticus* Monod, 1933 (extant); *A. cornishorum* Schweitzer and Feldmann, 1999 (fossil); *A. gallardoi* Serène and Soh, 1976 (extant); *A. globosa* (Karasawa, 1990) as *Tritodynamia* (fossil); *A. hexagonum* Rathbun, 1909 (extant); *A. microspinosus* new

species (fossil); *A. urretae* Schweitzer and Feldmann, 2001a (fossil).

Diagnosis.—Carapace trapezoidal, length to width ratio ranging from 0.63–0.87, averaging about 0.71; front downturned, axially sulcate, bilobed in extant forms, straight in fossil forms, about 20 percent maximum carapace width; fronto-orbital width to width ranging from 0.45–0.70, averaging about 0.59; anterolateral and posterolateral margins confluent; fronto-orbital width to posterior width about 1.00 in extant forms, about 0.80 in fossil forms; posterior width about half maximum carapace width; epigastric region square, inflated; cardiac region well-defined; branchial region may have broadly inflated epibranchial ridge forming a ridge, may be developed as a narrow ridge just posterior to epibranchial region, or may lack ornamentation.

Discussion.—Schweitzer and Feldmann (2001a) reviewed the genus and the occurrences of the subfamily Asthenognathinae in the fossil record. In addition to the characters discussed above under the subfamily, some fossil species of *Asthenognathus* differ from extant species in some ways. Extant species of *Asthenognathus*, as well as other extant members of the subfamily, have fronto-orbital width to posterior width ratios of about 1.00, while the three fossils for which this measure is available have much lower ratios, 0.74–0.85. Schweitzer and Feldmann (2001a) found that the ratio of the fronto-orbital width to posterior width was an important character in differentiating between members of the Hexapodidae Miers, 1886, and other decapods with similar dorsal carapace morphology. This is, therefore, a significant difference between the fossil and extant species. In addition, extant members of *Asthenognathus* have a bilobed front that is axially sulcate. The bilobed nature ranges from being very distinct in dorsal view in *A. inaequipes* to less distinctive in *A. atlanticus*. In the fossil species in which the front is preserved, it is straight and axially sulcate. Thus, there appears to be a trend from straight fronts to more distinctly bilobed fronts through time. Two fossil members of *Asthenognathus*, *A. urretae* and *A. microspinosus* new species, have a broad epibranchial ridge extending from the anterolateral corner obliquely to the cardiac region. The extant *A. atlanticus* has a very narrow ridge in the branchial area, appearing to be just posterior to the position of the epibranchial region (Monod, 1956, p. 384, fig. 541). Further, *A. inaequipes* appears to have a broadly swollen epibranchial region, although it is not developed into a distinctive ridge as in the two fossil species (Sakai, 1976, pl. 203). Thus, the development of the epibranchial ridge is variable in both extant and fossil species of the genus.

All of these exceptions indicate that *Asthenognathus* as currently understood is a variable genus. Considerable variation exists in the length/width, fronto-orbital width to width, and fronto-orbital to posterior width ratios as well as in the nature of the front and the epibranchial region. As shown, however, there are gradations in the nature of

Table 4.—Carapace ratios and other characteristics of species of all species of *Asthenognathus*, except *A. hexagonum* Rathbun, 1909, for which information is not known, and *A. gallardoi* Serène and Soh, 1976. * Measurements taken from specimens illustrated in Monod (1956). L = maximum length; W = maximum width; FOW = fronto-orbital width; PW = posterior width; F = frontal (rostral) width.

Species	L/W	FOW/W	FOW/PW	PW/W	F/W	Front	Epibranchial region
<i>A. atlanticus</i> Monod, 1933, specimen 1*	0.67	0.59	1.07	0.55	0.25	Bilobed	narrow ridge
<i>A. atlanticus</i> Monod, 1933, specimen 2*	0.73	0.56	1.29	0.44	0.27	Bilobed	narrow ridge
<i>A. atlanticus</i> Monod, 1933, specimen 3*	0.67	0.58	1.00	0.58	0.24	Bilobed	narrow ridge
<i>A. cornishorum</i> Schweitzer and Feldmann, 1999	0.71	0.7	0.8	0.51	0.15	Unknown	none
<i>A. globosa</i> (Karasawa, 1990)	0.73	—	—	—	0.2	Unknown	none
<i>A. inaequipes</i> Stimpson, 1858	0.69	0.45	1.00	0.45	0.17	Bilobed	broad ridge, weak
<i>A. microspinus</i> new species	0.87	0.54	0.85	0.54	0.23	Straight	broad ridge
<i>A. urretae</i> Schweitzer and Feldmann, 2001a	0.66	0.7	0.74	0.57	0.16	Straight	broad ridge

the front and epibranchial regions. Further, examination of the characters of each species (Table 4) demonstrates that there is no clear means by which to separate the genus into two or more genera. There is too much overlap in characters between various species.

Further complicating the effort is the fact that members of the Chasmocarcininae Serène, 1964 of the Goneplacidae MacLeay, 1838, have dorsal carapace morphologies almost identical to asthenognathines (Schweitzer and Feldmann, 2001a). The best means by which to differentiate members of the Chasmocarcininae and the Asthenognathinae is by the nature of the sternum; chasmocarcinines have a distinctive supplementary plate between sternites 7 and 8 which is unique to the group. Without the sternum, it may be nearly impossible to determine if species are chasmocarcinines or asthenognathines. The fossil specimens discussed here as well as those referred to *A. cornishorum* and *A. urretae* do not have the supplementary plate and are clearly not members of the Chasmocarcininae. We opt to retain all of the fossil and extant species currently assigned to *Asthenognathus*, even in light of the considerable variation in various characters of the dorsal carapace (Table 4). We believe that this will best demonstrate the affinities of these animals, which are clearly closely related and are demonstrably not members of the Chasmocarcininae.

Thus far, the oldest known species of the genus is *Asthenognathus microspinus*, middle Oligocene in age, described here. *Asthenognathus urretae* was reported from the Centinela Formation, near Calafate, Argentina, then thought to be Eocene in age (Casadío, Feldmann et al., 2000; Schweitzer and Feldmann, 2001a). Newer information suggests that the Centinela Formation is most likely late Oligocene–early Miocene in age (Casadío et al., 2000; Guérstein et al., in press), making that species about the same age as *A. cornishorum* from Washington, USA (Schweitzer and Feldmann, 1999). *Asthenognathus globosa* is known from early Miocene rocks in Japan (Karasawa, 1990; 1993). Thus, the genus displayed an amphitropical distribution throughout its early history. The new species does not greatly expand the geographic range of the genus. Extant members of the genus inhabit the Atlantic Ocean from France to North Africa (Monod, 1956; Manning and Holthuis, 1981), and the Indo-Pacific

(Rathbun, 1909; Sakai, 1976). The early amphitropical distribution and the modern tropical distribution suggest that the genus was dispersed via Tethyan routes and currently displays a relict Tethyan distribution.

Asthenognathus microspinus, new species (Fig. 8)

Types.—Holotype GHUNLPam 25.043, paratypes GHUNLPam 25.044–25.073; paratypes MSNM i23463–i23468; paratypes CM 52508–52513; CM52519, cast of MSNM i25468; CM 52520, cast of MSNM i28466; CM 52521, cast of MSNM i25463; CM52526, cast of GHUNLPam 25.062; CM 52527, cast of GHUNLPam 25.065; CM 52528, cast of GHUNLPam 25.049; CM 52529, cast of GHUNLPam 25.052; CM 52530, cast of GHUNLPam 25.061.

Diagnosis.—Carapace only slightly wider than long, L/W = 0.87; surface finely granular, granules coarsest near posterior margin; rostrum deflexed, straight, axially sulcate; anterolateral margin with tiny, closely spaced spines; epigastric region broadly inflated into ridge.

Etymology.—The trivial name is derived from the Greek words *mikros*, meaning small, and *spinos*, meaning spine, referring to the tiny spines on the anterolateral margin, unique among members of the genus.

Description.—Carapace trapezoidal, slightly wider than long, L/W = 0.87, widest just anterior to posterolateral reentrant; flattened transversely and moderately vaulted longitudinally; surface granular, granules coarsest posteriorly.

Fronto-orbital width occupying entire anterior margin of carapace; rostrum downturned, extending slightly beyond orbits, maintaining width along entire length, anterior margin straight, axially sulcate dorsally, about 23 percent maximum carapace width; orbits directed slightly axially, rimmed, margins sinuous, fronto-orbital width about 54 percent maximum carapace width; frontal width to fronto-orbital width ratio about 0.43.

Anterolateral and posterolateral margins continuous, anterolateral portion ornamented by small, sharp, closely spaced spines; posterolateral reentrants large, smooth, rimmed; posterior margin straight, rimmed, about 63 percent maximum carapace width, fronto-orbital width about 85 percent posterior width.

Epigastric regions square, markedly inflated; mesogastric region well-defined posteriorly, anterior process weakly marked; protogastric and hepatic regions poorly differentiated from one another; urogastric region well-defined, long, with concave margins; cardiac region triangular, apex directed posteriorly, round swellings at each point of triangle; intestinal region flattened, poorly differentiated. Epibranchial region inflated to form a ridge, beginning at anterolateral corner and

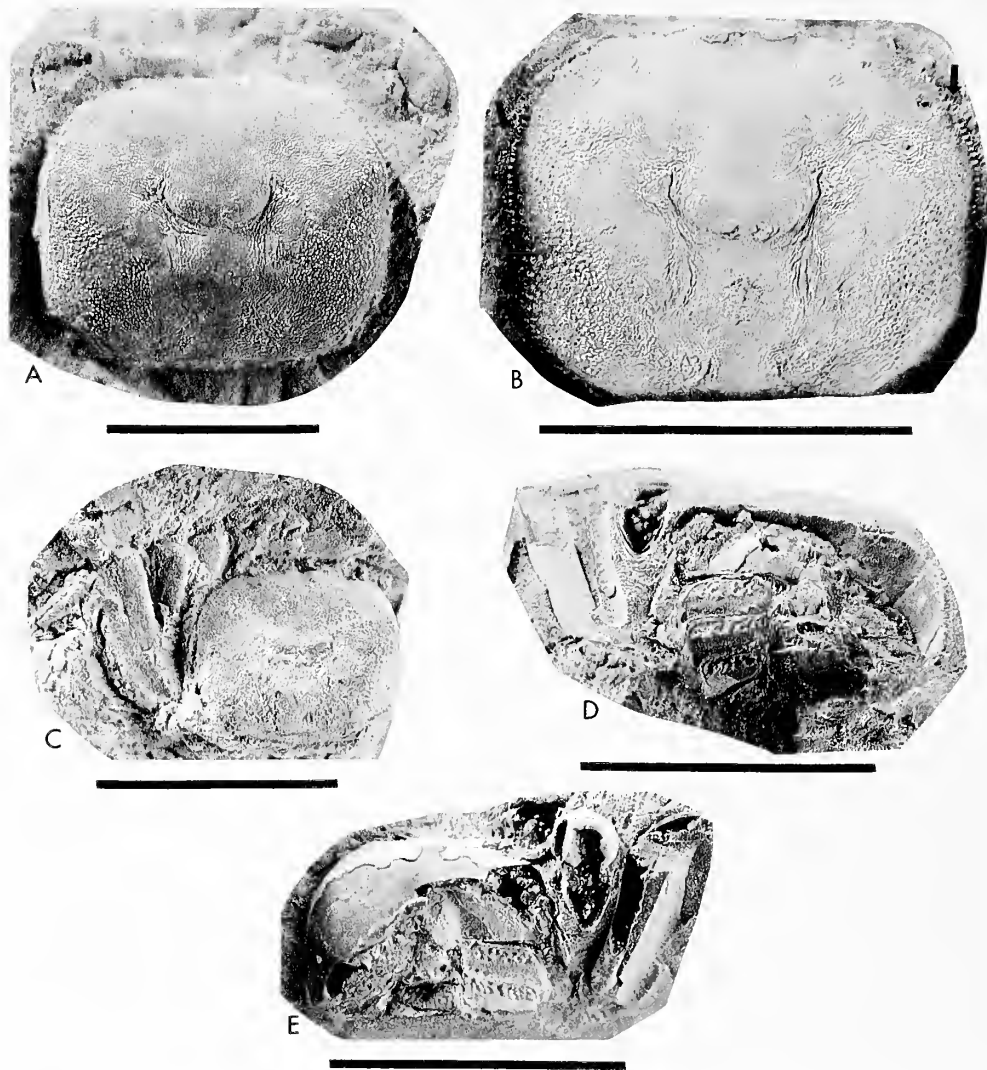


Fig. 8.—*Asthenognathus microspinus*. A. Dorsal carapace, paratype MSNM i25466; B. Dorsal carapace, holotype, GHUNLPam 25.043, arrows indicate tiny spines on anterolateral margin; C. Dorsal carapace and appendages, paratype GHUNLPam 25.061; D. Ventral view of sternites and portion of male abdomen, paratype GHUNLPam 25.047 (part); E. Ventral view of sternites, GHUNLPam 25.047 (counterpart). Scale bars equal to 1 cm.

extending to anterior margin of cardiac region; remainder of branchial region undifferentiated.

Thoracic sternites 4–6 with parallel upper and lower margins, each sternite granular anteriorly. Chelipeds short, chelae stout; meri of pereopods 2 and 3 long, slender.

Measurements.—Measurements (in mm) taken on specimens of *Asthenognathus microspinus* are in Table 5.

Discussion.—*Asthenognathus microspinus* new species closely resembles the characteristics that define the genus with a few exceptions, as discussed above. Distinctive features of the new specimens demonstrate that they should be considered as a new species. The posterolateral re-entrants of *A. microspinus* are deeper and better-defined than those in other species. Undoubtedly, the most distinguishing difference between *A. microspinus* and all other species of the genus is the

presence of small spines on the anterolateral margin (GHUNLPam 25.043). These are unique among members of the genus.

The cardiac region of *A. microspinus* new species is transversely hexagonal, while that of other species is semi-circular in shape (Monod, 1956; Karasawa, 1993; Schweitzer and Feldmann, 2001a). The mesogastric region in *A. microspinus* is well-defined by grooves posteriorly and poorly defined anteriorly, while *A. inaequipes* and *A. atlanticus* have better defined anterior portions of the mesogastric region (Monod, 1956; Sakai, 1976). The epibranchial region of *A. microspinus* is broadly inflated and ridge-like, while *A. atlanticus*, *A. cornishorum*, and *A. inaequipes* lack this quality (Monod, 1956; Schweitzer and Feldmann, 1999; Schweitzer and Feldmann, 2001a). *Asthenognathus cornishorum* pos-

Table 5.—Measurements (in mm) taken on specimens of *Asthenognathus microspinus* new species.

Specimen	Width	Length	Posterior width	Fronto-orbital width	Frontal width
GHUNLPam 250.49	11.4	9.0	6.4	—	—
CM 52511	10.2	8.7	5.7	5.1	2.2
CM 52510	8.1	7.7	—	—	—
CM 52508	11.1	10.1	7.0	—	—
CM 52513	9.5	7.7	5.9	—	—
GHUNLPam 25.043 Holotype	12.8	11.1	7.8	6.8	2.7
MSNM i25468a	11.5	10.0	7.1	6.0	2.6
GHUNLPam 25.065	11.4	10.3	—	5.4	2.5
MSNM i25463	9.0	7.8	5.7	4.8	2.2
GHUNLPam 25.044	9.2	8.2	5.9	5.1	2.5
MSNM i25465	11.3	9.4	6.8	—	—
MSNM i25466	12.6	10.8	8.4	6.5	2.6
GHUNLPam 25.061	8.2	7.6	4.8	—	—
GHUNLPam 25.062	11.2	9.5	7.1	—	—
GHUNLPam 25.045	8.1	7.0	5.4	4.7	2.0
GHUNLPam 25.046	7.7	7.3	6.0	5.0	1.9

sesses a row of granules parallel to the posterior margin (Schweitzer and Feldmann, 1999), not present on the new species. The carapace of *A. urretae* is ornamented with setal pits, not present on the new species, and *A. urretae* possesses a tiny spine in the posterolateral re-entrant not present in the new species. The carapace of *A. globosa* is more densely granular and the granules are larger than the granules present on the new species (Karasawa, 1990, 1993).

Indeterminate Cheliped (Fig. 7C)

Material Examined.—Specimen MSNM i23017.

Description.—Manus of cheliped longer than high, H/L about 0.65, becoming higher distally, bulbous, moderately vaulted longitudinally and highly vaulted from upper to lower margin; proximal margin oriented obliquely, making about 70 degree angle with lower margin; upper and lower margins convex; distal margin appearing to be relatively straight.

Fixed finger extending in straight line from manus, lower margin straight, narrowing markedly distally. Movable finger narrowing distally.

Carpus of cheliped bulbous, not much longer than high, H/L about 0.90; proximal margin strongly convex; lower margin short, convex; upper margin weakly convex; distal margin nearly straight, rimmed.

Remainder of cheliped unknown.

Measurements.—Measurements, in mm, taken on MSNM i23017: maximum length of manus (L), 12.5; maximum height of manus (H), 8.1; maximum length of carpus (L), 6.4; maximum height of carpus (H), 5.8.

Discussion.—The material is insufficient to make any taxonomic judgement. More material will be necessary to resolve the identity of this specimen; we report it because it differs from all other material described herein and thus represents a separate taxon.

DISCUSSION

The number of fossil decapod species reported from Argentina has increased dramatically in recent years (Feldmann et al., 1995; Schweitzer and Feldmann, 2000a, b, c, 2001a). Interestingly, the faunas of individual rock units, even those of roughly equivalent age, are remarkably different from one another. Of the decapods described from localities in the Late Oligocene–early Miocene Centinela Formation near Estancia 25 de Mayo, near Calafate, Santa Cruz Province, three genera, *Asthenognathus*, *Munida*, and *Proterocarcinus*, are shared with the fauna of the middle Oligocene Río Foyel Formation, collected near Bariloche, about 500 km to the north. Notably, the Río Foyel Formation decapods are just as similar to the fauna of the late Oligocene–early Miocene Pysht Formation of Washington, USA; the two units share three genera, including *Asthenognathus*, *Callianopsis*, and *Trichopeltarion* (Schweitzer-Hopkins and Feldmann, 1997; Schweitzer and Feldmann, 1999).

Clearly this pattern deserves detailed investigation, in progress by two of us (RF and CS); at the least, this pattern of shared decapod genera supports the Oligocene age suggested for the Patagonian rock units.

Two species described herein represent the oldest known occurrences of their respective genera, *Trichopeltarion levis* and *Asthenognathus microspinus*, suggesting that these two genera originated in the middle to high southern latitudes with subsequent dispersal to more northern latitudes. Such an origination and dispersal pattern was originally described by Zinsmeister and Feldmann (1984) and was expanded upon by Schweitzer (2001). Currently, at least five genera with this origination and dispersal pattern are known, including *Palaeopinnixa* Via, 1966; *Chasmocarcinus* Rathbun, 1898; *Calappa* Weber, 1795; *Trichopeltarion*; and *Asthenognathus* (Feldmann and Zinsmeister, 1984; Feldmann and Wilson, 1988; Schweitzer and Feldmann, 2001a; Schweitzer, 2001). The pattern

originally described by Zinsmeister and Feldmann (1984) continues to be supported by fossil evidence.

Decapods collected from late Miocene rocks of Península Valdés are currently under study by some of us (SC, RF, AP, and CS), and these rocks share few genera with either the Centinela or Foyel formations. One or both of the two most commonly encountered genera in southern South America, *Chaceon* and *Proterocarcinus*, are found in each of the units mentioned here and are also abundant in all units in which they occur, so apparently they were highly successful ecological generalists during the Oligocene–late Miocene.

Proterocarcinus is the only genus common to both Maastrichtian–Danian rocks (Feldmann et al., 1995) and late Oligocene–early Miocene rocks of southern Argentina. The composition of the decapod fauna in southern Argentina therefore diverged greatly during the Paleocene–Oligocene interval, probably due to changes in sea level and in circulation patterns due to continued continental breakup. Clearly, the paleoenvironmental situation in southern South America was conducive to the evolution of diverse and specialized decapod faunas. Resolution of these issues is ongoing (SC, RF, AP, and CS).

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NEW MATERIALS OF *DIMETRODON TEUTONIS* (SYNAPSIDA: SPHENACODONTIDAE)
FROM THE LOWER PERMIAN OF GERMANY

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ABSTRACT

Additional specimens of the sphenacodontid synapsid *Dimetrodon teutonis*, including a maxilla, dorsal vertebrae, scapulocoracoids, a humerus, and partial, articulated hindlimbs that consist of the epipodials, tarsi, and incomplete digits, not only expand significantly its known anatomy, but also confirm its recognition as a new species of *Dimetrodon*. The new materials, like the holotype, are from the Lower Permian Tambach Formation, lowermost formation of the Upper Rotliegend Group or Series, of the Bromacker quarry locality in the midregion of the Thuringian Forest near Gotha, central Germany, and represent the only record of the genus outside of North America. The original estimated weight of 14 kg for the holotype of *D. teutonis*, calculated on the basis of centra size, is revised to 24 kg for the larger, more fully mature, newly discovered specimens. This is still significantly less than the calculated maximum of nearly 37 kg for the smallest, previously recognized species, *D. natalis*. Linear measurements of appendicular elements also indicate a substantial size difference between the two species.

KEY WORDS: Sphenacodontidae (*Dimetrodon*), Lower Permian, Upper Rotliegend, Bromacker locality, Germany

INTRODUCTION

Until recently, occurrences of the best known basal or pelycosaurian-grade synapsids, the dominant predator *Dimetrodon*, were restricted to the Lower Permian of North America, where remains of its 12 currently recognized species are commonly encountered (Romer and Price, 1940; Reisz, 1986). A much wider distribution of *Dimetrodon*, however, was realized with the description (Berman et al., 2001) of a new species, *D. teutonis*, based on a single, adult specimen consisting of a series of 14 thoracic vertebrae from the well-known Bromacker quarry locality, an area of once active commercial sandstone quarries located in the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend Group or Series, in the middle region of the Thuringian Forest, near Gotha, central Germany. Undoubtedly, the most notable and easily recognized feature of *Dimetrodon* is its possession of an extraordinarily high dorsal sail supported by the elongation of the vertebral neural spines. The holotype of *D. teutonis* was of particular interest in having an estimated total body

weight, determined using a methodology based on centrum size that was first formulated and employed by Romer and Price (1940) and Romer (1948), of only 14 kg, which is only half that of the smallest, previously described species, *D. natalis*. It was reasoned (Berman et al., 2001), on the basis of sphenacodontid phylogeny, that the diminutive size of *D. teutonis* represents an autapomorphy, which appears to be in accord with an apparent absence of size-dominant, basal synapsid predators at the Bromacker. The diminutive size of *D. teutonis* was interpreted as a probable adaptation to a truly terrestrial, relatively upland existence like that proposed for the Bromacker locality, which was located near the center of a small, internally drained paleograbben (Eberth et al., 2000). Here, *D. teutonis* is envisioned as having preyed on small vertebrates, as well as possibly large invertebrates, in an assemblage that was dominated in both size and abundance by herbivorous diadectids and where large predators were rarely encountered (Berman et al., 1998; 2003). Newly discovered, slightly larger, more

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fully mature specimens of *D. teutonius* contribute significantly to its known anatomy, provide additional evidence for its generic assignment and recognition as a new species, and allow reassessment of its maximum weight as the smallest of the known species of the genus.

The following acronyms are used to refer to institutional repositories of specimens: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNG, Museum der Natur, Gotha,

Germany; UM, Museum of Paleontology, University of Michigan, Ann Arbor.

Anatomical structures are identified by the following abbreviations: ac, anterior coracoid; as, astragalus; c, lateral centrale; ca, calcaneum; fi, fibula; pc, posterior coracoid; r, rib; sg f, supraglenoid foramen; ti, tibia; tri c, coracoid process for attachment of coracoid head of triceps muscle; v, vertebra; 1–5, distal tarsals one through five.

SYSTEMATIC PALEONTOLOGY

Class Amniota

Order Synapsida Osborn 1903

Suborder Eupelycosauria Kemp 1982

Family Sphenacodontidae Williston 1912

Genus *Dimetrodon* Cope 1878

Dimetrodon teutonius Berman et al. 2001

Revised Diagnosis.—Autapomorphies distinguishing *Dimetrodon teutonius* from all other members of the genus include: 1) diminutive size, with a calculated maximum weight of 24 kg compared to nearly 37 kg for the otherwise smallest, previously recognized species, *D. natalis*; 2) relatively smaller height and length of the dorsal centra; 3) free marginal outline of the anterior coracoid formed by an unusually long, straight, dorsal margin that meets the anterodorsally curving ventral margin in a sharply acute angle. Primitive features of the maxilla distinguishing *D. teutonius* from all other members of the genus except perhaps *D. natalis* include: 1) marginal tooth formula of two precanines, two canines, and 15 postcanines, as compared to a formula of three, two, and 15, respectively, in *D. natalis*; 2) ventral margin slightly convex; 3) little or no indication of a dorsally arching, maxillary step at the anterior end of the ventral margin.

Holotype.—MNG 10598 consists of a series of 14 loosely associated vertebrae represented by at least some portion of the centrum and neural spine and considered to approximate serial positions 8–21 of the presacral column and, therefore, possibly all thoracic vertebrae.

Referred Specimens.—MNG 10654, partial right scapulocoracoid, greater part of left scapular blade, nearly complete left humerus, and partial, articulated hindlimbs that include epipodials, tarsus, metatarsals, and a few proximal phalanges, with the left also represented by a counterpart impression; MNG 10655, probable posterior dorsal vertebrae that includes three articulated vertebrae and a closely associated fourth with the neural spines either missing or incomplete; MNG 10693, four articulated probable middorsal vertebrae, two of which possess complete neural spines, with three associated left ribs, and several scattered, partial vertebrae and ribs, and the greater part of the left scapulocoracoid with counterpart impression; MNG 13433, right maxilla with dorsal lamina preserved as impression.

Horizon and Locality.—Lower Permian Tambach Formation, lowermost formation of the Upper Rotliegend Group or Series, of the Bromacker quarry locality in the midregion of the Thuringian Forest near the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany. Two superimposed stratigraphic successions that can be characterized by their facies associations are informally referred to as the Lower Beds and Upper Beds (Eberth et al., 2000). All of the vertebrates from the Bromacker quarry come from the Upper Beds, which consist of alluvial paleochannel and sheetflood facies and lacustrine suspension deposits. The vertebrates are almost exclusively restricted to two massive, red-brown, very fine-grained sandstone and siltstone sheetflood facies that are separated by 50 cm in a stratigraphic interval of 1.2 m. The holotype MNG 10598 was collected from the upper sheetflood, whereas the referred specimens MNG 10598, 10654, and 13433 and MNG 10655 and 10693 are from the upper and lower levels, respectively.

DESCRIPTION AND ASSIGNMENT TO *DIMETRODON*

Included in the new materials referable to *Dimetrodon teutonius* is the first cranial element, an isolated right maxilla (Fig. 1) that conforms exactly to the sphenacodontid pattern. It is exposed in lateral view, and, whereas it is essentially complete along its ventral margin, including most of the dentition, the dorsal lamina is represented by an impression that faithfully preserves its full extent. The slightly convex ventral margin of the maxilla has a maximum length of 82 mm. The dental series includes 19 teeth or their spaces, consisting of two precanines, two canines, and 15 postcanines; it is

possible, however, that an additional tooth may have been present at either end of the series. The precanines decrease serially in size anteriorly from a maximum length of 7 mm. Of the canine pair, only the basal half of the posterior tooth is preserved, but it suggests an approximate length of 10 to 12 mm. The lengths of postcanines increase serially in size posteriorly to about their mid-series from about 4 to 6 mm, then steadily decrease to about 2 mm at the end of the series. In sphenacodontid fashion, all the teeth are slightly to moderately recurved and laterally compressed, particularly the postcanines,

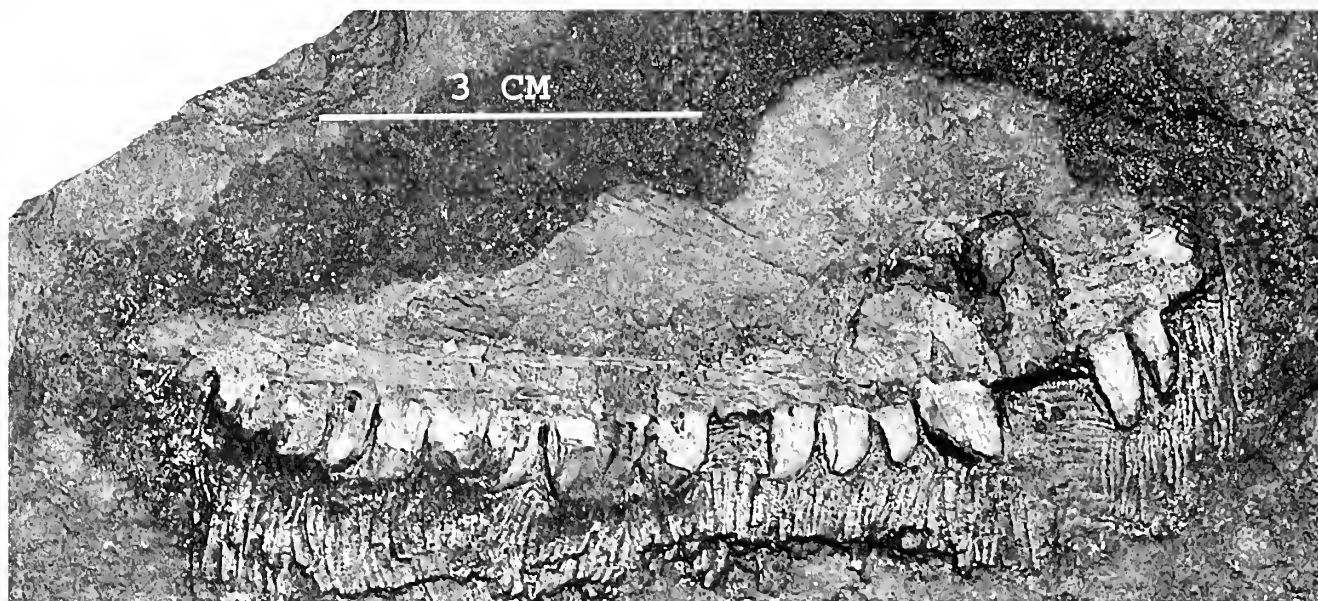


Fig. 1.—*Dimetrodon teutonis*. Right maxilla MNG 13433 in lateral view with dorsal lamina preserved as impression.

with moderately developed, anterior and posterior cutting edges without serrations, and the postcanines have a slightly bulbous appearance compared to the other teeth. There is a pronounced lateral swelling and increased height of the alveolar shelf to accommodate the roots of the canines. Although the anterior end of the ventral margin may not be complete, there is no indication that it arched dorsally to form a maxillary “step” like that seen in the larger species of *Dimetrodon* (Romer and Price, 1940). The height of the dorsal lamina suggests that, as in all sphenacodontids, it contacted the anterior portion of the lateral or ventral margin of the nasal, shortening the lacrimal anteriorly and preventing it from reaching the external naris.

The vertebrae of MNG 10655 and 10693 (Fig. 2), which appear to be from the posterior and mid-region of the presacral column, respectively, neither deviate in any noticeable way from those in the holotype of *Dimetrodon teutonis* nor provide any distinguishing features about the species (Berman et al., 2001). This, in addition to their exact conformation to the pattern exhibited by the majority of *Dimetrodon* species, eliminates the need to describe them. What is relevant about the new specimens, however, is that they are slightly larger than those of the holotype, indicating a greater overall body size or weight (see COMPARISONS AND DISCUSSION section below). An overall increase in size also is expressed in the height of the neural spines. Of the four articulated middorsal vertebrae in MNG 10693, only the anterior-most two possess complete neural spines, with the lengths of the first and second being 280 and 326 mm, respectively. However, considering the incompleteness of the preserved presacral column and the marked

difference in the lengths of the two complete spines, the longest-spined vertebra(e) may not be represented.

Of the three partially preserved scapulocoracoids, two include the greater portions of the scapula and the anterior and posterior coracoids: a right of MNG 10654 exposed in lateral view (Fig. 3A) and a left of MNG 10693 exposed in medial view (Fig. 3B). In both the missing marginal areas, particularly of the coracoid plate, are partially indicated by a lighter-colored, reduced matrix caused by its contact with the bone. Fortunately, the counterpart block of the scapulocoracoid of MNG 10693 (Fig. 3C) preserves precisely nearly the entire extent of the girdle as impression and in the lighter-colored, reduced matrix caused by contact with the bone. The scapulocoracoid of *Dimetrodon teutonis* is unmistakably of the pattern for the genus. This is especially evident in the outline of the scapular blade, which is narrow and waisted strongly toward its base. The lateral opening of the supraglenoid foramen is positioned, as in other sphenacodontids, a short distance anterior to the supraglenoid buttress. The sutures between the three elements of the scapulocoracoid are closed and undetectable. Closure of the sutural contacts with the posterior coracoid is particularly suggestive of advanced maturity, inasmuch as this bone typically remains loosely attached until an extremely late stage of development in sphenacodontids (Romer and Price, 1940). The coracoid process for the triceps muscle is well developed, which also suggests maturity. The counterpart impression of MNG 10693 reveals the outline of the free margins of the anterior coracoid, which is distinctly different from those of other basal synapsids (see COMPARISONS AND DISCUSSION section below) in being formed

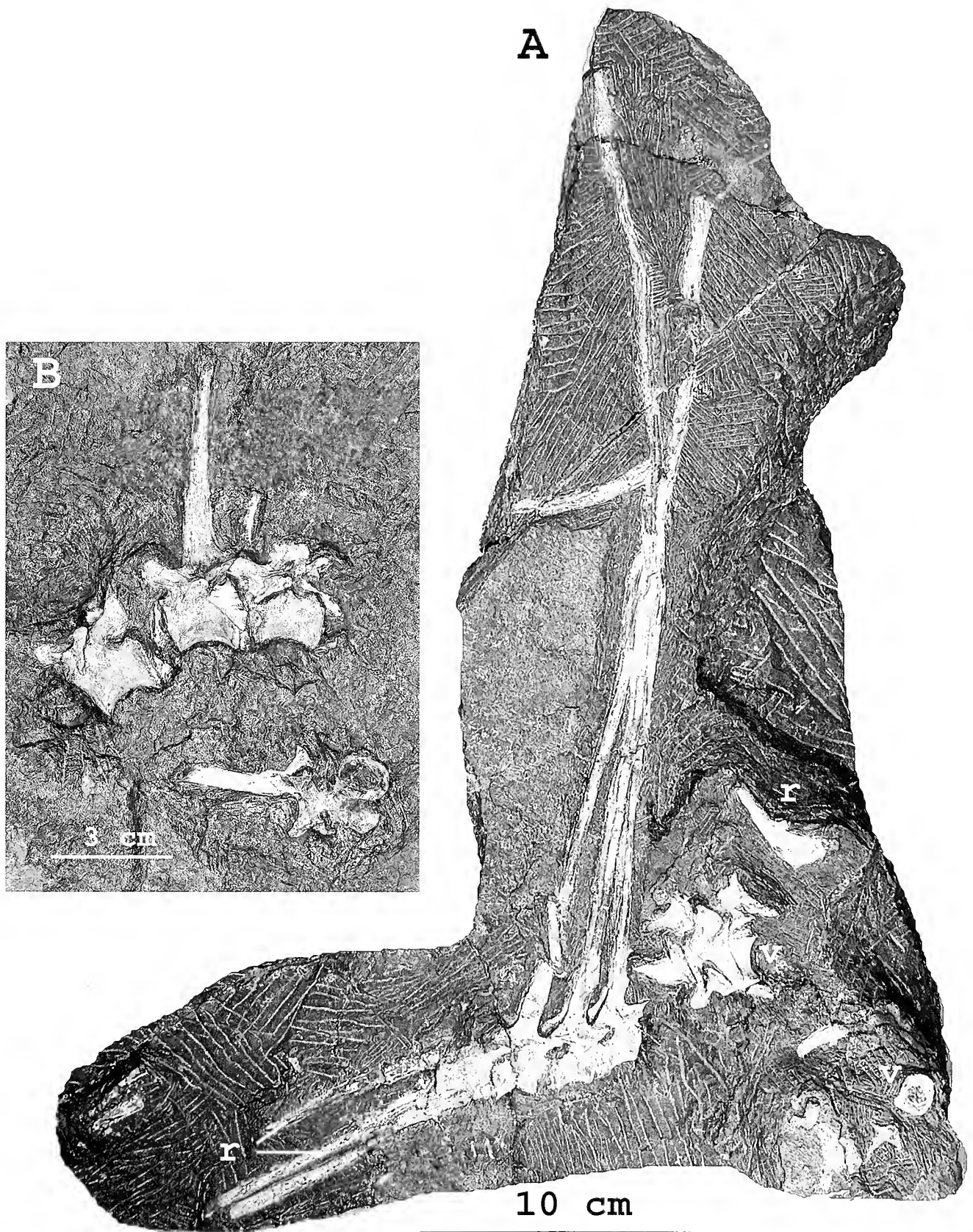


Fig. 2.—*Dimetrodon teutonix*. A. Middorsal vertebrae and ribs of MNG 10693. B. Probable posterior dorsals of MNG 10655.

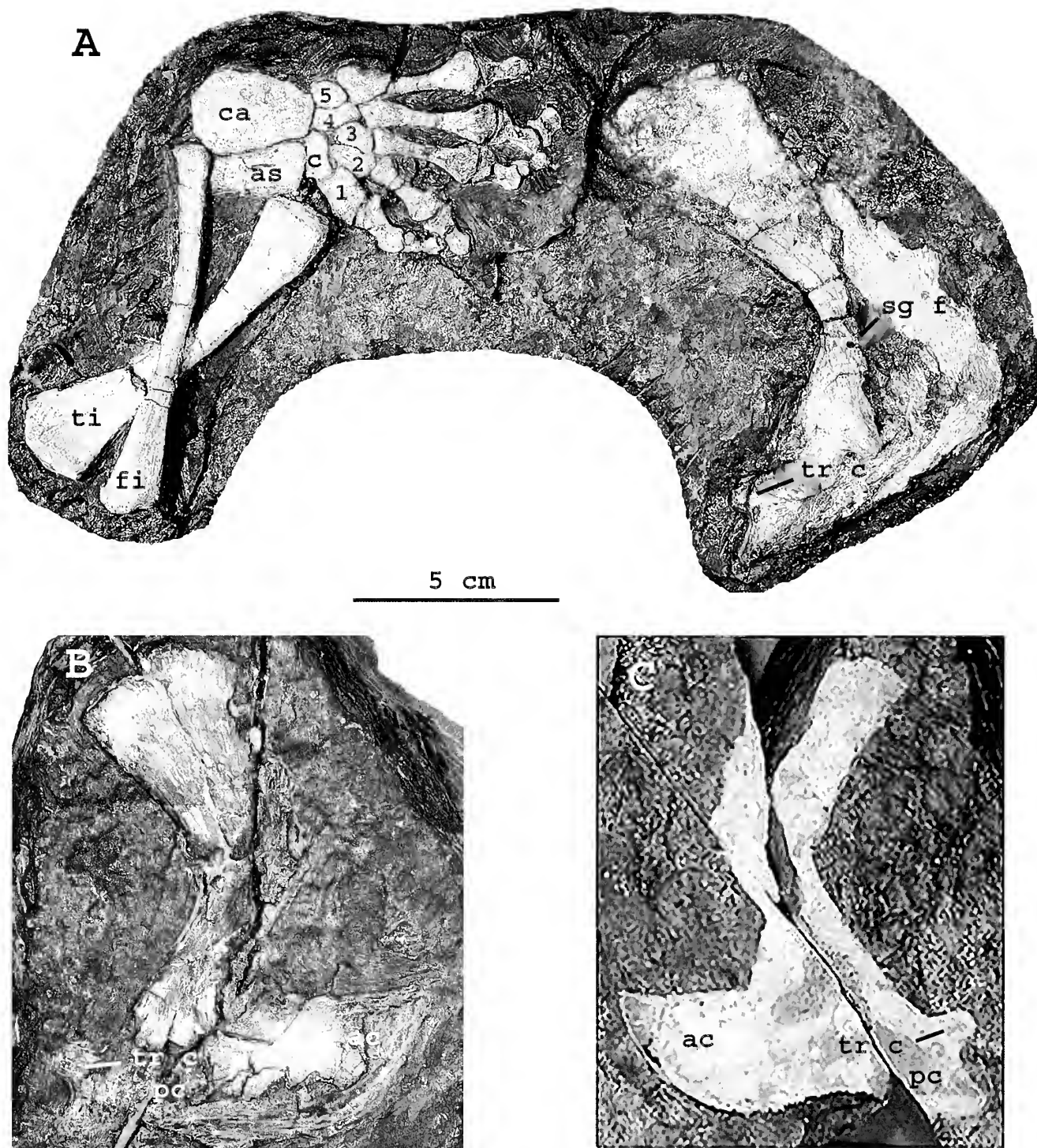


Fig. 3.—*Dimetrodon teutonis*. A. Partial right scapulocoracoid in lateral view and partial right hindlimb of MNG 10654 that includes the epipodials, tarsus except for probable loss of medial centrale, metatarsals, and a few phalanges in ventral view except for lateral or posterior view of fibula. B. Left scapulocoracoid MNG 10693 in medial view. C. Counterpart block showing nearly its entire extent as impression and by the lighter-colored, reduced matrix caused by contact with the bone of its medial surface.



Fig. 4.—*Dimetrodon teutonis* MNG 10654. A. Dorsal, and B. Ventral views of left humerus (proximal head toward top of page).

by a long, straight, horizontal dorsal margin that meets the anterodorsally curving ventral margin in a sharply acute angle.

The single preserved humerus of *D. teutonis*, a left belonging to MNG 10654 (Fig. 4), is nearly complete, missing mainly the supinator process and the entepicondyle, though the latter portion has been almost entirely restored using its impression in the matrix as a natural mold to cast it in epoxy. Despite some surface bone erosion, it is evident that the processes and articular surfaces were well developed and, therefore, indicative of a fully mature individual. In overall structure the humerus is indistinguishable from those of other species of *Dimetrodon*.

The partial, articulated hindlimbs of MNG 10654 are exposed mainly in ventral view and include the epipodials, tarsi, metatarsals, and a few proximal phalanges. Although the ventrally exposed elements of the left hindlimb are too incompletely preserved and badly weathered to allow description, they are represented by a nearly complete, counterpart impression, whereas those of the right are well preserved (Fig. 3A) and permit the following observations. The well-ossified tibia, exposed in ventral or medial view (flexor surface), and fibula, exposed in lateral or posterior view, offer no basis for challenging a *Dimetrodon* assignment. The ventrally exposed pes is well

ossified, and the tightly fitting tarsal elements are indicative of advanced maturity. The tarsus is complete except for the possible loss of a very small medial centrale that would have been positioned medial to the lateral centrale. The pes of *D. teutonis* exhibits no features contradictory to a *Dimetrodon* assignment, and several features are recognized as collectively distinctive of the genus: 1) the horizontal arm of the L-shaped astragalus is extremely short, giving the element a narrowly rectangular outline; 2) the calcaneum is less flared laterally, widening slightly toward its proximal end rather than at its midlength; 3) the large, proximodistally narrow, subrectangular lateral centrale extends across nearly the entire articular face of the distal end of the astragalus; 4) the first distal tarsal is very large, subequal to that of the fourth, and has an exceptionally broad contact with the first metatarsal; 5) the proximal margin of the fourth distal tarsal is limited in contact to the calcaneum and is excluded from contact with the astragalus by the lateral centrale; 6) the distal half of the medial and lateral surfaces of the fourth distal centrale are deeply incised to receive the tightly fitting third and fifth distal tarsals; 7) the proximal head of the first metatarsal is greatly expanded to accommodate its contact with the comparably expanded first distal tarsal; and 8) the metatarsals increase in length serially to the fourth, which is subequal to that of the fifth.

COMPARISONS AND DISCUSSION

In the description of the holotype of *Dimetrodon teutonis*, based solely on a series of 14 presacral vertebrae believed to be dorsals approximating serial positions 8–21, it was considered remotely possible that the vertebrae might belong to the rare, closely related Early Permian sphenacodontid *Secodontosaurus*. Although the cranial anatomies of *Secodontosaurus* and *Dimetrodon* are easily distinguished from one another (Reisz et al., 1992), their postcrania share some notable similarities, particularly the vertebrae in possessing elongated neural spines that supported a high, dorsal sail (Romer and Price, 1940). However, as was noted (Berman et al., 2001) in the description of the holotype of *D. teutonis* and is reaffirmed here by the referred specimen MNG 10693, the cross-sectional outline of the distal portion of the dorsal neural spines in *D. teutonis* conforms within the narrow range of variation described in other members of the genus (except in *D. milleri*) in being transversely expanded into a distinct figure-eight pattern, whereas in *Secodontosaurus* it is subcircular, though retaining the fore and aft longitudinal grooves.

Most importantly, the new materials referred to *D. teutonis*, particularly the maxilla, scapulocoracoids, and pedes, are not only strongly characteristic of *Dimetrodon*, but the former two are quite distinct from not only those of *Secodontosaurus*, but other basal or pelycosaurian-grade synapsids (Reisz et al., 1992; Romer and Price, 1940). In its overall shape and dentition the maxilla in *D. teutonis* is typical of the genus and easily distinguished from that in *Secodontosaurus*: 1) the maxilla in *D. teutonis* reaches a greatest height at its anterior end of about 33% of the bone's length, which is close to the 40 to 50% values for the other species. The smaller height of the maxilla in *D. teutonis* is probably a primitive feature (Reisz et al., 1992). In stronger contrast, however, the relatively long, low maxilla in *Secodontosaurus* reaches a greatest height at its midlength that is only about 16% of its length; 2) the differentiation of the 19 total maxillary teeth in *D. teutonis* into two precanines, two canines, and 15 postcanines conforms to the range of counts for the genus in which a total of 13 to 20 maxillary teeth includes zero to three precanines, two canines, and 10 to 15 postcanines. This is quite distinct from the range of values for *Secodontosaurus* in which a total tooth count of 21 to 26 may include as many as six precanines, two canines, and 17 postcanines. In addition, the teeth in *Secodontosaurus* are in general relatively more slender, sharply pointed, and widely spaced, with frequent gaps that Romer and Price (1940) suggested might indicate a difference in the type of tooth succession. Several features of the scapulocoracoid in *Secodontosaurus* distinguish it from that in *Dimetrodon*: 1) the scapular blade is relatively shorter and broadens greatly at its dorsal end; 2) the free margin of the anterior coracoid

forms a broadly expanded, semicircular plate; and 3) the coracoid process for the coracoid head of the triceps muscle is lower, broader, and less pronounced. It is also relevant to point out here that MNG 10654 and 10693 demonstrate the association of the scapulocoracoids and pedes with the *Dimetrodon*-like vertebrae. Taken together, the above observations are considered irrefutable evidence for the correctness of the generic assignment of the holotype and referred specimens of *D. teutonis*. Furthermore, the only other basal synapsids identified, but as yet undescribed, from the Bromacker quarry are a varanopid and caseid (Berman et al., 2003). Both are represented by essentially articulated, postcranial skeletons, one of the former and two of the latter, which are easily distinguished from that of *Dimetrodon*.

It was demonstrated (Berman et al., 2001) that the holotype of *Dimetrodon teutonis* represents an adult by comparing its vertebrae with the dorsals of a juvenile specimen of an indeterminate species of *Dimetrodon* (MCZ 2027). Although both specimens are of comparable size, several features easily distinguished the latter as a juvenile: 1) presence of neurocentral sutures or the disarticulation of the centra from the neural arches; 2) much narrower transverse width of the basal portion of the neural spine; and 3) cross-sectional outline of the distal portion of neural spine is oval with an anteroposterior length that slightly exceeds the transverse width, rather than being transversely expanded with a figure-eight outline that is typical of *Dimetrodon*, including *D. teutonis*. Not only do the vertebrae, but also the other postcranial elements of the new, slightly larger specimens referred to *D. teutonis* exhibit features indicative of an adult stage of development: 1) the complete closure and fusion of the sutures of the scapulocoracoid bones, particularly those with the posterior coracoid, and the well-developed coracoid process of the posterior coracoid; 2) the well-developed processes and articular facets of the limb elements; and 3) the fully ossified, tightly articulated elements of the tarsus.

With an estimated weight of 14 kg, it was the diminutive size of the holotype of *Dimetrodon teutonis* that was cited (Berman et al., 2001) as the primary character distinguishing it from the smallest, previously recognized member of the genus, *D. natalis*, having an estimated weight of 28 kg (Romer and Price, 1940). The recognition that the new specimens described here represent individuals larger than the holotype, based on linear measurements of the postcranial elements, allows a recalculation of the adult size and weight of *D. teutonis*. However, as pointed out by Romer and Price (1940) and Romer (1948), comparisons between the 12 closely related, recognized species of *Dimetrodon* on the basis of linear proportions is complicated not only by subtle differences in their proportions, but also by the fact that

they exhibit a general, progressive increase in size with greater upward stratigraphic occurrence. Recognizing the need for a standard unit of measurement in comparing interspecific linear dimensions of primitive synapsids, Romer and Price (1940, p. 8) proposed and employed what they termed the orthometric linear unit (OLU). Simply stated, linear measurements are expressed in values relative to the animal's overall size, in which one orthometric linear unit, $r^{2/3}$, is defined as equal to the radius of an average-sized dorsal centrum to the $2/3$ powers. Their derivation of the OLU was based on the following reasoning: 1) if the vertebral column suspended between the shoulder and pelvic girdles is considered to support the greater part of the animal's weight, the roughly circular, cross-sectional area of the dorsal centrum should be directly proportional to the animal's weight as the square of the radius; and 2) if the animal's volume, which is directly related to body weight, is theoretically the cubed totals of all its linear measurements, then the lengths of any given portion of the body should be directly proportional to the cube root of the cross-sectional area of centrum. The utility of the OLU of measurement as an accurate means of comparison between closely related species of similar ontogenetic growth stages has been demonstrated clearly by Currie (1978).

In arriving at the OLU, Romer and Price (1940) based their calculation on the transverse diameter or width at the posterior end of the average-sized dorsal, which for *Dimetrodon natalis* was 14 mm. Judging from their table of vertebral measurements for numerous museum specimens (Romer and Price, 1940, table 3), however, a maximum of 16 mm was recorded in two specimens of *D. natalis* (UM 9667 and 16201), which undoubtedly more accurately depicts the maximum size or weight attained by this species. Obviously, if a comparison between the sizes and weights of fully adult specimens of *D. natalis* and *D. teutonis* is sought, then the preferred measurements of the dorsal vertebrae of both species would be their maximums. Although vertebral centrum length and transverse width measurements are limited to a few vertebrae in MNG 10655 and 10693, their respective values of 18 and 13 mm are very consistent and greater than the average values of 14.3 and 9.9 mm, respectively, for the dorsal centra in the holotype MNG 10598. Most importantly, the maximum values for *D. teutonis* are still notably less than those given by Romer and Price (1940) for *D. natalis* of 27 and 16 mm, respectively. When converted to OLUs the maximum length and width values of 6.75 and 4.00, respectively, for *D. natalis* exceed substantially those of 5.17 and 3.48, respectively, for *D. teutonis*. Whether using direct linear measurements or OLUs, the maximum vertebral dimensions of *D. teutonis* are definitely smaller than those of *D. natalis*. Using these revised, maximum values for the transverse width of the dorsal centrum, a marked difference in the overall body sizes or weights of the two species can also be demonstrated that utilizes the same

method employed by Romer and Price (1940) for estimating total weights of *Dimetrodon* species and other basal synapsids. Initially they used the classical technique of measuring the volume of liquid displaced by a model, which in this instance was based on a nearly complete skeleton of a presumed female of *D. limbatus*. The weights of other species of *Dimetrodon* were then calculated on the premise that r^2 of the OLU is an index of relative weight. On the basis of this reasoning, the revised, maximum weights of *D. teutonis* and *D. natalis* are approximately 24 and 38 kg, respectively. Although based on maximum centrum-width values, their estimated weights are still exceeded by the 41 and 47 kg of the otherwise smallest species of *Dimetrodon*, *D. occidentalis* and *D. milleri* (the latter calculated for a presumed smaller female), respectively, which are based on average-sized dorsals (Romer and Price, 1940; Berman, 1977).

Of the series of four articulated middorsal vertebrae of MNG 10693, one possesses a spine length of 326 mm, and, although it may not represent the maximum for that individual, it exceeds substantially the 245 mm for the longest spine in the holotype (Berman et al., 2001). When converted to OLUs the spine length measurement increases from 90 to about 94, possibly suggesting some disproportional increase in sail height with maturity. However, the new OLU value for sail height in *D. teutonis* duplicates those of 95 and 94 of the slightly larger *D. occidentalis* and *D. milleri* (unfortunately sail height is not available for *D. natalis*, because complete middorsal spines are not known; Romer and Price, 1940), indicating that in the smallest *Dimetrodon* species sail height or size appears to have kept pace with the increase in general body size. On the other hand, Romer (1948) clearly demonstrated that in the much larger and later occurring species, with estimated body weights ranging from 70 to 250 kg, there is a dramatic, disproportional increase in sail size, with OLU values ranging from a little over 100 to 250.

In terms of direct linear measurements, a comparison between the appendicular elements of *Dimetrodon teutonis* and those recorded for *D. natalis* by Romer and Price (1940; table 4), clearly indicates that the former is much smaller. The range of measurements given by Romer and Price for the height of six scapulocoracoids of *D. natalis*, measured from the top of the anterior end of the glenoid to the top of the blade, is 85–114 mm, whereas in *D. teutonis* this measurement for the right of MNG 10654 is 93 mm. The lengths given by Romer and Price for 51 humeri, 33 tibiae, and 15 fibulae have ranges of 99–133, 72–113, and 85–115 mm, respectively, whereas those for the left humerus and right tibia and fibula of *D. teutonis* MNG 10654 are 100, 88, and 88 mm, respectively. These differences are even more meaningful considering that the measurements for the elements of *D. teutonis* probably represent maximums, or near maximums, of fully mature individuals.

A combination of several plesiomorphic features of the maxillae of *D. teutonis* and *D. natalis* distinguish them

from all other members of genus: 1) a greater number of marginal teeth that includes in *D. teutonis* two precanines, two canines, and 15 postcanines, with *D. natalis* differing only in its possession of three precanines, which is not considered specifically significant; 2) ventral margin slightly, rather than strongly, convex; 3) a height-to-length ratio of one third, and 4) little or no indication of a dorsally arching, maxillary step at the anterior end of the ventral margin. Among the new materials of *D. teutonis* is one element, an anterior coracoid, which easily distinguishes it from not only all other sphenacodontids, but also all basal synapsids in which this element is known.

As precisely exemplified by the counterpart impression and the lighter-colored, reduced matrix that contacted the bone of the medial surface of the left scapulocoracoid of MNG 10693 (Fig. 3C), the free, marginal outline of the anterior coracoid is unique in having an unusually long, straight, horizontal dorsal margin that meets the antero-dorsally curving ventral margin in a sharply acute angle, rather than being of the standard, basal synapsid shape of a broadly expanded, semicircular plate (Romer and Price, 1940). Unfortunately, neither an illustration nor an adequately preserved example of this element is available for *D. natalis*.

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ON THE CRANIAL OSTEOLOGY OF THE YELLOW ARMADILLO *EUPHRACTUS SEXCINCTUS*
(DASYPODIDAE, XENARTHRA, PLACENTALIA)

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ABSTRACT

The external surfaces of the bones of the skull of the yellow armadillo *Euphractus sexcinctus* are described in detail based on six museum specimens (five from the Carnegie Museum of Natural History, the last from the Field Museum). Soft-tissue structures (e.g., nerves, arteries, veins, and muscles) are reconstructed onto the skulls based on a serially sectioned, 105-mm crown rump length yellow armadillo fetus (also from the Field Museum). One osteological specimen, a juvenile, retains sutures in the basicranium fused in the adults, which confirm the presence of a compound auditory bulla (with entotympanic and ectotympanic elements), a long anterior process of the malleus forming the lateral border of the Glaserian fissure, and a well-developed postglenoid process of the squamosal forming the anterolateral surface of the tubular external acoustic meatus (the postglenoid process has been reported as absent in extant xenarthrans). To place the cranial osteology of the yellow armadillo in a phylogenetic context, the morphology of 58 soft-tissue conduits (e.g., grooves, canals, and foramina) are compared among *E. sexcinctus*, the dasypodid *Dasypus kappleri*, the bradypodid *Bradypus variegatus*, the myrmecophagids *Tamandua tetradactyla* and *T. mexicana*, the dog *Canis familiaris*, the Eocene palaeonodont *Metacheiromys* sp. and *M. simpsoni*, the Oligocene leptictid *Leptictis dakotensis*, and the Late Cretaceous stem placental *Zalambdalestes lechei*. Of the conduits considered, 11 distinguish *Euphractus sexcinctus*; 16 distinguish Dasypodidae; 12 distinguish Pilosa; 5 distinguish *Bradypus variegatus*; 4 distinguish *Tamandua*; 13 distinguish Xenarthra; and 4 distinguish Xenarthra + *Metacheiromys*. Noteworthy results within the *E. sexcinctus* sample are plasticity in number, size, and position both between and within individuals in some nervous and vascular foramina (e.g., the foramina on the palate for the major, accessory, and palatine nerves and vessels, the foramina in the squamosal, parietal, and frontal for the rami temporales of the stapedia artery).

KEY WORDS: *Euphractus*, Dasypodidae, Xenarthra, skull, osteology, foramina

INTRODUCTION

In 1975, McKenna proposed that edentates or xenarthrans, the South American anteaters, sloths, and armadillos, were the first group to be separated from all other placentals, which he included in the newly named cohort Epitheria. This hypothesis was supported by the retention of primitive anatomical and physiological characters in xenarthrans that were lost or modified in epitheres. The purported primitive characters of xenarthrans identified by McKenna (1975) have been criticized by others (e.g., McNab 1978, 1985; Novacek 1982; Wible et al. 1990; Gaudin et al. 1996). Nevertheless, the xenarthran-epithere dichotomy has received at least tentative support from additional studies on neuroanatomical (Kirsch et al. 1983) and other morphological characters (Novacek 1986, 1990; Novacek and Wyss 1986; Novacek et al. 1988; Shoshani and McKenna 1998). Linked to Xenarthra in the studies by Novacek and co-authors are the Pholidota, the Old World pangolins. Some studies of molecular data have also provided support for the xenarthran-epithere split (de Jong et al. 1985; Miyamoto and Goodman 1986; Czelusniak et al. 1990; Waddell et al. 1999). In fact, some recent analyses of DNA sequences that identify four major placental lineages—two from the Southern Hemisphere, Xenarthra and Afrotheria, and two from the Northern Hemisphere, Laurasiatheria and Euarchonta + Glires—have iterations that place Xenarthra at the placental base (Madsen et al.

2001; Murphy et al. 2001a; Scally et al. 2001; Delsuc et al. 2002). In each of these studies pangolins are grouped with carnivorans and not xenarthrans. However, other recent analyses including DNA sequence data result in no support for the xenarthran-epithere split (Murphy et al. 2001b; Arnason et al. 2002; Asher et al. 2003).

Elsewhere we (Gaudin et al. 1996) have presented a critique of the non-neural morphological characters purported to support the xenarthran-epithere dichotomy. In addressing that topic, we were struck by the dearth of detailed reports on the cranial osteology of xenarthrans. If Xenarthra does indeed fall at the base of Placentalia, then an understanding of their morphology is essential for phylogenetic studies of relationships among epitheres (see Maddison et al. 1984; Nixon and Carpenter 1993). Addressing the lack of descriptive studies combined with the potential critical phylogenetic position of xenarthrans is the impetus for the current report on the cranial anatomy of the extant yellow or six-banded armadillo *Euphractus sexcinctus*.

Living armadillos of the family Dasypodidae include eight genera and 21 species (Wetzel 1985; Gardner 1993; Vizcaino 1995). Two species, *Cabassous centralis* and *Dasypus novemcinctus*, have distributions into Central America with the latter extending into the southern United States; the remainder is confined to South America. The monotypic *Euphractus sexcinctus* is

found in the savannas of southern Suriname and their continuation in adjacent Para, Brazil, as well as Mato Grosso and the highlands of Brazil, Uruguay, Paraguay, northern Argentina, and southeastern Bolivia (Wetzel 1982, 1985; Redford and Wetzel 1985). *E. sexcinctus* is allocated to the dasypodid tribe Euphractini by most authors (e.g., Simpson 1945; Wetzel 1985; McKenna and Bell 1997), along with the hairy armadillo *ChaetophRACTUS* and the pichy *Zaedyus*. Based on a study of the allometry of cranial proportions in armadillos, Moeller (1968) modified the Euphractini to also include the pichiciego *Chlamyphorus*, which traditionally is separated in its own subfamily. Engelmann (1985) presented results similar to those of Moeller based on cladistic analysis of morphological characters, which considered some fossil armadillos but did not include a character matrix. Delsuc et al. (2002) analyzed three nuclear gene sequences for the extant armadillo genera except *Chlamyphorus*. They reported three distinct lineages, dasypodines at the base of Cingulata, and tolpeutines (*Priodontes*, *Cabassous*, and *Tolpeutes*) and euphractines (*ChaetophRACTUS*, *Euphractus*, and *Zaedyus*). *Euphractus* was allied with *Zaedyus*, but relationships within both euphractines and tolpeutines were characterized by extremely short internal branches, low maximum likelihood bootstrap supports, and moderate Bayesian posterior probabilities. In fact, Delsuc et al. (2003) added two mitochondrial genes to the previous analysis with similar results, except that they favored ties between *Euphractus* and *ChaetophRACTUS*. We (Gaudin and Wible, in press) have completed a phylogenetic analysis of 163 craniodental characters among the eight extant armadillo genera and eleven genera of extinct armadillos, pampatheres, and glyptodonts. Analyses of extant taxa only and of all taxa identified a monophyletic clade of the euphractines of Moeller (1968); in the latter analysis, *Zaedyus* and *Chlamyphorus* were identified as sister taxa at an unresolved trichotomy with *Euphractus* and *ChaetophRACTUS*.

Some very significant contributions to the anatomy of the armadillo head are already in the literature. The cartilages, bones, and muscles of the head at various prenatal stages have been described for *Dasypus noveuncinctus* (Parker 1885; Fawcett 1921; Edgeworth 1923; Reinbach 1952a, 1952b; Werner 1960) and the hard tissues only for *Zaedyus pichiy* (Reinbach 1955). However, these studies have included little about adult anatomy. The most detailed descriptions of the hard and soft tissues of the adult head are on *Chlamyphorus truncatus* (Hyrtl 1855; Macalister 1873; K  hlhorn 1965; Segall 1976), a fossorial form that is probably blind (Wetzel 1985) and is perhaps the most specialized of extant armadillos. Murie's (1874) treatise on *Tolpeutes uatacus* (= *T. coumrus*) is another noteworthy contribution, which considers both hard and soft tissues. Unfortunately, these anatomical treatises lack detailed illustrations of most features.

Studies dedicated to soft-tissue systems have been published: the cranial arterial pattern in *Dasypus noveuncinctus* (e.g., Hyrtl 1854; Tandler 1899; Bugge 1979), *ChaetophRACTUS villosus* (= *Dasypus villosus*, Tandler 1899), and *Euphractus sexcinctus* (= *Dasypus setosus*, Tandler 1901); and muscles of the head in *D. noveuncinctus* and *E. sexcinctus* (e.g., Uekermann 1912; Smith and Redford 1990). Finally, the hard tissues of the ear region have been described for armadillos by various authors (e.g., Kampen 1905; Klaauw 1931; Guth 1961; Patterson et al. 1989). Nevertheless, the problem remains that a bone-by-bone description of the adult skull with consideration of the occupants of major foramina is not available for any extant armadillo.

MATERIALS AND METHODS

The following specimens of *Euphractus sexcinctus* were examined for this report.

(1) FMNH 28350 (Figs. 1–5, 7, 8A, 9A, 10A)—Adult skull with lower jaws from Descalvados, Mato Grosso, Brazil. Viewed under a stereomicroscope, this was the principal specimen providing details of cranial osteology for all external surfaces for the descriptions and illustrations. Additionally, the right auditory bulla was removed by someone prior to our study, allowing access to the middle-ear cavity. This well-preserved specimen shows details of sutural relationships and even retains the cartilaginous nasal septum. Drawings of the basicranium, left posterior braincase, and occiput of this specimen have been published in Patterson et al. (1989, fig. 5).

(2) FMNH E28532 (Figs. 11–17)—Fetus in alcohol from Descalvados, Mato Grosso, Brazil; 105 mm crown-rump length; 31 mm head length. In the Department of Anatomical Sciences and Neurobiology of the University of Louisville School of Medicine, Kentucky, the head was removed, decalcified, and serially sectioned at 15 µm. Sections were floated onto 934 slides and stained with Masson trichrome. Viewed under a compound microscope, this slide series provided details of soft-tissue anatomy as well as of the morphogenesis of cartilages and bones.

(3) CM 6398 (Figs. 8B, 9B, 10B)—Adult skull with lower jaws from Santa Cruz, Bolivia.

(4) CM 6399 (Figs. 8C, 9C, 10C)—Adult skull with lower jaws from Santa Cruz, Bolivia.

(5) CM 10743 (Figs. 8D, 9D, 10D)—Immature skull with lower jaws from Santa Cruz, Bolivia. This specimen, the smallest skull studied, preserved sutural information on the basicranium not available in the remaining sample.

(6) CM 61426 (Figs. 8E, 9E, 10E)—Adult skull with right mandible from Fazenda San Martin, Mato Grosso, Brazil.

(7) CM 101007 (Figs. 8F, 9F, 10F)—Adult skull with lower jaws from Exu, Pernambuco, Brazil.

Choice of terminology is a key step in anatomical description. Unfortunately, we cannot direct the reader to a single source for the anatomical terminology that we employ. Our first choice is to use English equivalents of terms in the *Nomina Anatomica* (fifth edition, 1983) and the *Nomina Anatomica Veterinaria* (fourth edition, 1994). However, these terms are not always the most appropriate, because they are devised for taxa (humans and domesticated mammals) exhibiting morphologies far removed from that of basal placentals and outgroups. In instances in which the *Nominae* are inadequate for depicting homologies across a broader range of taxa, we use what we believe are the best terms from the current comparative literature. Appendix 1 is a table of the anatomical terms used here with references and equivalents. Some terminology is from our own publications on aspects of the cranial anatomy of extinct and extant mammals (Wible 2003; Wible et al. 2004; Gaudin and Wible, in press), specifically, the cranial vasculature (Wible 1984, 1986, 1987; Wible and Rougier 2000) and the auditory region (Wible 1990; Patterson et al. 1992; Gaudin 1995, 2004). Perhaps the aspect of armadillo cranial anatomy with the most confused terminology is the facial musculature, as various authors (e.g., Windle and Parsons 1899; Uekermann 1913; Edgeworth 1923; Smith and Redford 1990) have used different terms in describing the same muscle. Before naming these muscles, their homologies across *Xenarthra* and outgroups should be evaluated, and that is beyond the scope of this report. Consequently, where appropriate we provide multiple muscle names. For the dental development terminology we follow Luckett (1993). For the taxonomic terms we follow Gardner (1993). Table 1 includes cranial measurements of the yellow armadillo specimens examined.

INSTITUTIONAL ABBREVIATIONS

CM—Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania

FMNH—Division of Mammals, Field Museum, Chicago, Illinois

USGS—United States Geological Survey Collection housed at United States National Museum, Smithsonian Institution, Washington, D.C.

USNM—United States National Museum, Smithsonian Institution, Washington, D.C.

UTCM—Mammal Collection, University of Tennessee at Chattanooga

YPM-PU—Princeton University Collection housed at Peabody Museum, Yale University, New Haven, Connecticut

DESCRIPTIONS OF CRANIAL BONES

Presented are bone-by-bone descriptions of the extracranial surfaces of the yellow armadillo skull, following the format employed by Wible (2003). The cranium of *Euphractus sexcinctus* FMNH 28350 is drawn in dorsal, lateral (with and without zygoma), ventral (with a close-up of the right ear region), and occipital views (Figs. 1–5) and the mandible in lateral, medial, and occlusal views (Fig. 7). For the sake of completeness, an illustration of the ear ossicles of *E. sexcinctus* by Guth (1961, fig. 87) is redrawn here (Fig. 6). Photographs of the crania in dorsal and ventral views and the mandibles in lateral views of FMNH 28350 and the CM sample are in Figures 8–10. Other useful figures of *Euphractus sexcinctus* already in the literature include the skull in lateral and ventral views (Grassé 1955, fig. 1129), the skull in lateral and oblique ventral views and the ear ossicles (Guth 1961, figs. 86, 87), and the basicranium in ventral, lateral, and posterior views (Patterson et al. 1989, fig. 5). We do not describe the dentition of *E. sexcinctus* here. Useful references on the dentition in adult armadillos include Sasso and Della Serra (1965), Ferigolo (1985), and Thenius (1989), and for dental ontogeny in *Dasyurus novemcinctus* see Martin (1916).

Also presented are schematic representations of seven cross sections of the fetal yellow armadillo FMNH E28532 to illustrate relationships between various hard- and soft-tissue structures (Figs. 11–17). Observations on the endochondral or intramembranous nature of a particular bone are based on the fetus.

Nasal

In the adult skull, the paired nasal bones are long and narrow; their maximum length is about 65% of the preorbital length in FMNH 28350. They form the osseous dorsal rim of the external nasal aperture and the bulk of the osseous roof of the nasal cavity (Figs. 1A, 2A). Underlying the intramembranous nasal bone is the roof of the cartilaginous nasal capsule, formed by the tectum nasi (shown in the fetus in Figs. 11, 12).

In the adult, the external sutural relationships of the nasal are as follows (Fig. 2A). Contacting the elongate lateral border are the premaxilla in front and the maxilla behind, and contacting the narrow posterior border is the frontal. The premaxilla forms less than half of the lateral border, and the edge of the nasal is slightly concave at its contact with the premaxilla. The maxillary contact is

straighter, but is angled medially toward the rear, with the widest point on the nasal just behind the premaxillary-maxillary suture in FMNH 28350 and CM 6398, 6399, and 10743 (Figs. 8A–D). In contrast, in CM 61426 and 101007, the nasals are angled laterally towards the rear, with the widest point on the nasal at the frontonasal suture (Figs. 8E, F). Laterally, the frontonasal contact is roughly horizontal, whereas medially there is a sharp v-shaped prong on the left and right frontals that extends forward between the nasals. The extent of the lateral part of the frontonasal contact differs among the specimens (Fig. 8). It is narrow and interdigitated in FMNH 29350 and CM 10743, narrow and irregular in CM 6398 and 6399, and wide and irregular in CM 61426 and 101007. At the external nasal aperture, a shallow u-shaped process of the nasals extends forward, contributing to the sizeable overhang of the external nasal aperture by the nasal visible in lateral view (Fig. 2C).

The dorsal surface of the nasal is convex, reflecting the oval cross-sectional shape of the nasal cavity. In the posterior part of the dorsal surface, near the maxillary border, several small foramina open into the substance of the nasal (Figs. 1A, 2A). On the left side of FMNH 28350, there are anterior and posterior foramen, both of which are posteriorly directed. On the right side of FMNH 28350, there is a corresponding posterior foramen, but anteriorly are two apertures that are slightly more rostrally positioned and more posterolaterally directed than the single anterior one on the left. The sectioned fetus has two small foramina in the posterolateral nasal that transmit veins that ultimately drain into the facial vein; the external nasal ramus of the ethmoidal nerve runs between the nasal and the tectum nasi. CM 61426 has two foramina, resembling the left side of FMNH 28350, and CM 101007 has three, resembling the right side of FMNH 28350. CM 6398 has four small foramina on the left and three on the right, and CMNH 6399 has one per side; both specimens have more than a dozen tiny foramina on the posterior part of the each nasal. An unnamed, small foramen occurs near the mid-length of the nasal and transmits a vein in the dog (Evans 1993) and humans (Clemente 1985).

In FMNH 28350, the rostral part of the ventral surface of the nasal is visible through the external nasal aperture (Figs. 1B, 2B). This part of the ventral surface can be described in medial and lateral parts. The ventral surface of the medial part exhibits the same contour as the corresponding dorsal surface, the two being separated by a thin layer of bone. The lateral part of the nasal, however, is roughly twice as thick and projects farther ventrally into the nasal cavity. Recessed somewhat from the external nasal aperture, the ventral surface of the lateral part bears a deep longitudinal trough, the full posterior extent of which is unknown. The medial wall of this trough forms a scroll, partially flooring the trough, which represents the ossified nasoturbinal. A similar trough, the dorsal

nasal meatus, occurs on the nasal in the dog and bears the nasoturbinal (Evans 1993).

Premaxilla

In the adult skull, the paired premaxillae form the lateral walls and floor of the anterior nasal cavity and the corresponding part of the rim of the external nasal aperture (Figs. 1A–C, 2). The premaxillae bear a single pair of teeth, the smallest of the upper dentition (Figs. 1B, 2B, 9). In the sectioned fetus, there is a single pair of tooth germs at a cap stage below the posterior part of the intramembranous premaxilla, just in front of the maxillary contact. For descriptive purposes, we treat the premaxilla as two components: palatal and facial.

In the adult, the palatal components of the left and right premaxillae (Figs. 1B, 2B) together are shaped like an arrowhead. The major features of the palatal components are the paired incisive foramina anteromedially and the paired premaxillary teeth posterolaterally. Demarcating the palatal from the facial component is a low ridge, which represents the inferior limit of the origin of a muscle inserting into the skin of the nose, the nasalis of Uekermann (1912) (shown in the fetus in Fig. 12). The ridge begins anteriorly at the midline just behind a very weak anterior spine, projects posterolaterally toward the premaxillary tooth, and becomes continuous with that tooth's lateral alveolar margin. Nestled between the arms of the v near its apex on either side of the midline are the elongate, narrow incisive foramina (Fig. 2B). The medial wall of the incisive foramen is formed by the laterally compressed palatine process of the premaxilla, which at the posterior end of the incisive foramen disappears into the nasal cavity dorsal to the body of the premaxilla. In the sectioned fetus, the anterior part of the incisive foramen transmits the nasopalatine duct (Fig. 12) and the posterior part the nasopalatine nerve along with a small companion artery and vein. In the adult, the premaxillary tooth and its alveolus are oval, with their main axis following the diagonal contour of the ridge demarcating the palatal and facial components of the premaxilla (Figs. 1B, 2B). Immediately posterior to the premaxillary tooth is the suture with the maxilla and then the alveolus for the first maxillary tooth. In the intervalveolar area, the premaxillary-maxillary suture runs slightly posteromedially, but on the palate it is angled anteriorly. The position of the premaxillary-maxillary suture differs in the studied sample (Figs. 1B, 2B, 9). At the midline, the suture lies near the midpoint of the premaxillary tooth in FMNH 28350 and CM 6398 and 61426. It is farther forward in CM101007, opposite the anterior edge of the premaxillary tooth on the right and halfway between that tooth and the incisive foramen on the left. In CM 6399 and 10743, the suture is just posterior to the incisive foramina.

The facial component of the premaxilla (Figs. 1C, 2C) is convex, reflecting the oval cross-sectional shape of

the anterior nasal cavity. Posteriorly, it contacts the maxilla at an irregular suture that runs dorsally from the interalveolar space and then angles forward dorsal to the slight bulge over the root of the premaxillary tooth. Superiorly, the premaxilla contacts the nasal at a curved suture in which the premaxilla is the convex member (Figs. 1A, 2A). Anteriorly at the external nasal aperture, the rim of the premaxilla has shallow medial and lateral concavities or notches in FMNH 28350 (Fig. 1B) and CM 101007. The smaller and shallower medial notch extends between the anterior nasal spine and a more pronounced projection, the sustentaculum of Wegner (1922); the lateral notch is between the sustentaculum and nasal bone. Medial and lateral notches are absent in CM 6399, 10743, and 61426, and this part of the premaxilla is damaged in CM 6398. Anterior to the bulge over the premaxillary tooth root are four to five small foramina in the surface of the facial component in FMNH 28350 (Fig. 2C); CM 6398, 6399, 61426, and 101007 have many more. The sectioned fetus has two small nutrient veins that drain from a comparable surface of the premaxilla ultimately into the facial vein.

Based on FMNH 28350, the dorsal surface of the premaxilla contacts three skeletal elements within the nasal cavity. Dorsal to the left and right anterior nasal spines are the paired "septomaxillae" (Fig. 2C). CM 101007, in which the "septomaxillae" are missing, has a small, shallow fossa just off the midline on the dorsal surface of the anterior nasal spine that housed the horizontal process of the "septomaxilla." Dorsal to the left and right palatine processes is the rostral tip of the vomer (shown in the fetus in Fig. 12). Lateral to the vomer, the anterior tip of the ossified maxilloturbinal rests on the premaxilla, and between the base of the maxilloturbinal and the premaxilla is a canal for the nasolacrimal duct (shown in the fetus in Fig. 12).

"Septomaxilla"

The paired "septomaxillae" are only preserved in FMNH 28350 (Figs. 2B, C, 9); their absence in the remaining specimens reflects the loose attachment of these elements to the skull. In ventral view (Figs. 2B, 9), these bones are roughly U-shaped in the adult, with the open end of the U pointing anteriorly. Following Wegner (1922), the intramembranous "septomaxilla" or os nariale can be divided into two major parts: the horizontal process at the base of the U and the interfenestral process at the tip. We place septomaxilla in quotes because it is likely not the homolog of the septomaxilla occurring in monotremes and various Mesozoic mammals (Wible et al. 1990, but see also Zeller et al. 1993).

The horizontal process is situated dorsal to the anterior nasal spine of the premaxilla and is only visible in ventral view (Fig. 2B). The ventral surface of the horizontal process is flat and nearly circular, except that its ante-

rior border is slightly concave. Only the posteriormost part of the horizontal process contacts the premaxilla immediately posterodorsal to the feeble anterior nasal spine. The dorsal surface of the horizontal process is not flat; its medial edge is curved dorsally and presents a broad medial facet that contacts the cartilaginous nasal septum, which is preserved in FMNH 28350. There is no contact with the "septomaxilla" of the opposite side. Based on the sectioned fetus, the dorsal surface of the horizontal process underlies the lamina anterior transversalis, the anteriormost floor of the nasal cartilages.

Extending from the anterolateral aspect of the horizontal process is a finger-like process, the pedunculus of Wegner (1922), which connects to the interfenestral process (Fig. 2B). The proximal part of the pedunculus is near vertical and bears a furrow on its posterolateral surface, which based on the sectioned fetus contacts the atrioturbinal. Where the furrow ends, there is a tiny spur on the posterior surface of the pedunculus, the pars facialis of Wegner (1922), and then the pedunculus bends anterodorsally at about 120 degrees. The part of the pedunculus distal to the bend is narrower and longer.

As the pedunculus approaches the roof of the nasal cavity, it broadens, more so along its dorsal border, into the flat, roughly heart-shaped interfenestral process, the apex of the heart being continuous with the pedunculus (Fig. 2B). The interfenestral process is obliquely oriented, with one surface facing ventrolaterally and the other dorsomedially. The cleft at the tip of the process bears a short, shallow, longitudinal sulcus on both surfaces. In the sectioned fetus, the interfenestral process of the "septomaxilla," which is not broadened, has an intimate relationship to the nasolacrimal duct (Fig. 11). The nasolacrimal duct enters the lacrimal foramen in the lacrimal and runs forward between the lateral wall of the nasal cavity and the facial processes of the maxilla (Fig. 13) and premaxilla (Fig. 12). At the level of the interfenestral process, the nasolacrimal duct moves medially, accompanied by a branch of the infraorbital nerve, artery, and vein. The duct passes ventral to the interfenestral process and runs forward a short distance ventromedial to the "septomaxilla," whereas the nerve, artery, and vein are situated ventrolaterally (Fig. 11). Near the tip of the interfenestral process, the nasolacrimal duct moves medially and enters the anterior nasal cavity.

Maxilla

The paired maxillae are sizeable elements in the adult skull; their greatest length is just under half that of the skull (Figs. 1B, C, 2B, C). They bear eight pairs of teeth, increasing in size through the first five and decreasing thereafter (Figs. 1B, 2B, 9). The outer contour of the teeth also changes from more oval anteriorly to nearly circular posteriorly, and the anterior teeth slant labially, the posterior ones linguallly. The sectioned fetus has seven pairs of

tooth germs in the intramembranous maxillae: the first six are at an early bell stage and the last at a cap stage. For descriptive purposes, the maxillae can be treated as having four parts: the facial, palatine, zygomatic, and orbital processes. A fifth part is the contribution of the maxilla to the lateral wall of the nasal cavity, but that is beyond the scope of this report.

In the adult, the facial process of the maxilla (Figs. 2A, C) forms the bulk of the nasal cavity's lateral wall as well as a small part of the roof, contacting the premaxilla anteriorly, the nasal anterodorsally, the frontal posterodorsally, and the lacrimal and jugal posteriorly at the root of the zygoma. A weak longitudinal ridge is present on the posterior two-thirds of the facial process (Fig. 2C). It is continuous posteriorly with a sharper ridge on the lacrimal and jugal, and divides the facial process into two parts. Dorsal to the ridge is the crescent-shaped contribution to the nasal roof. Its surface is rough, in particular at its lateral margin, and bears more than a dozen tiny foramina in all specimens studied (Figs. 1A, C), presumably for nutrient veins, although none are present in the corresponding part of the sectioned fetus. Ventral to the ridge is the facial process's contribution to the lateral nasal wall. The ventral part of this surface, immediately above the teeth, is the near vertical alveolar margin, which then flares dorsolaterally to join the ridge. The amount of flaring increases posteriorly, grading into the zygoma and contributing to the triangular outline of the rostrum in ventral and dorsal views (Figs. 1A, B). The flaring on the facial process and zygoma produces a shelf of increasing width dorsolateral to the alveolar margin of the first six maxillary teeth (Fig. 2B). The major occupants of this mainly concave surface, the antorbital fossa (Fig. 2C), as seen in the sectioned fetus, are a muscle that arises from the ridge, and the infraorbital nerve and vessels. The muscle is variously identified as the retractor naris (Windle and Parsons 1899), the maxillo-labialis and levator labii superioris alaeque nasi (Uckermann 1912), the zygomaticus (Edgeworth 1923), the maxillonasolabialis (Edgeworth 1935), and the nasolabialis (Smith and Redford 1990). It sends four tendons into the tip of the nose and upper lip (three of which are visible and one labeled in the fetus in Fig. 12) and has a small area of attachment on the orbicularis oris muscle. In addition, arising from this shelf, at the level of the second and third tooth germs in the fetus, is a muscle that passes into the posterior part of the upper lip, the caninus muscle of Uckermann (1912). Within this shelf, at the level of the front of the fifth maxillary tooth in the adult (the fourth tooth germ in the fetus) is the infraorbital foramen (Figs. 2B, C). It is U-shaped in ventral view (Figs. 2B, 9), nearly circular in anterior view, and slanted anterodorsally from the side. In a slightly curved line anterodorsal to the infraorbital foramen are a half dozen or so ventrolaterally directed openings in the facial process in all specimens studied (Fig. 1C). In the fetus, there are a similar number

of apertures in a comparable position, all of which transmit nutrient veins. The two most posterior ones also transmit what appear to be superior alveolar rami of the infraorbital nerve and the second from the front a branch of the infraorbital artery.

The palatine processes of the maxillae (Fig. 2B) contribute to the floor of the nasal cavity and are the largest components of the hard palate, though accounting for less than half the surface area. They meet on the midline at the intermaxillary suture, which extends from opposite the middle of the premaxillary tooth to just behind the middle of the fifth maxillary tooth. At that level, the palatine processes of the maxillae meet the palatine bones at an inverted U-shaped suture, and only a narrow strip of the maxilla forms the medial alveolar margin of the more posterior teeth. The palatine process of the maxilla ends behind the last tooth as the maxillary tuberosity, which has a roughened surface, in particular on its lateral aspect (Fig. 3A). Attached there and along the lateral margin of the last two tooth germs in the fetus is the buccinator muscle (Fig. 13); Uckermann (1912) states that this muscle arises from the outer side of the alveolar process in the adult, but does not limit it to specific tooth positions. The adult palatine processes are not flat, but are curved anteroventrally, contributing to the downward keel of the rostrum in lateral view (Fig. 2C). Medial to the second through fifth maxillary teeth in the palatine processes are more than a dozen foramina of varying sizes and at varying distances from the teeth in FMNH 28350 (Fig. 4) and CM 6398, 61426, and 101007; fewer are present in CM 10743. CM 6398 differs in that there is one pair of foramina, opposite the second maxillary tooth, that are much larger than the others and with very deep sulci extending from them anteriorly to the level of the first maxillary tooth. CM 6399 has two such pairs of foramina. The more posterior and lateral pair is opposite the anterior part of the third tooth on the right, and the gap between the third and fourth tooth on the left. The sulci from these foramina extend forward to the back half of the second tooth and the gap between the second and third tooth, respectively. The more anterior and medial foramina are located opposite the gap between the second and third tooth on the right, and the middle of the third tooth on the left. The sulci for these extend forward to the premaxillary-maxillary suture opposite the first upper tooth. There are a half dozen or so foramina in the sectioned fetus, all of which transmit branches of the major palatine nerve and half of which also transmit branches of the major palatine vessels. These foramina open into a longitudinal palatine canal for the major palatine nerve and vessels within the maxilla (Fig. 13) that continues posteriorly into the palatine bone.

The zygomatic process of the maxilla (Fig. 2B) is a stout, digitiform element continuous with the facial process in front and the orbital process behind. As seen in the lateral view (Fig. 2B), it is angled posteroventrally at

about 45 degrees to the vertical, with its posterior border opposite the midpoint of the sixth maxillary tooth. The zygomatic process has two surfaces, anteroventral (Fig. 3A) and posterior (Fig. 2B), and forming the dorsal border of both is the lacrimal proximally and the jugal distally. The anteroventral surface is narrower than the posterior, because the jugal's contribution is broader on the anterior than posterior side of the zygoma. The posterior surface of the zygomatic process is smooth, but the anteroventral surface has a low ridge running approximately down its middle (Fig. 1C). On and dorsal to this ridge is the attachment of the maxillonasolabialis muscle in the fetus. At the ventrolateral tip of the anteroventral surface is a roughened process that continues posterolaterally onto the jugal (Fig. 1B). Attached to this prominence in the fetus is the superficial masseter muscle (labeled in the adult in Fig. 2B). Running through the base of the zygomatic process is the infraorbital canal. Its posterior opening, the maxillary foramen (Fig. 3A), is nearly circular, dorsal to the sixth maxillary tooth, and slightly larger than the anterior opening, the infraorbital foramen. There are several small foramina in the medial wall of the infraorbital canal in all specimens studied; the fetus has one that transmits a superior alveolar nerve and vessels.

The orbital process of the maxilla (Fig. 3A) forms roughly half of the medial wall of the anterior orbit, the bulk of the remainder being completed by the orbital process of the frontal. The maxilla's contacts in the orbit are with the lacrimal dorsally at the zygomatic root, the frontal dorsally, and the palatine posteroventrally. The suture with the frontal is irregular and slanted such that the maxilla's orbital contribution is narrower posteriorly. The suture with the palatine is very short, situated posterodorsal to the maxillary tuberosity behind the last tooth. Dorsal to the palatamaxillary suture is a sizeable recess, where the maxilla lies wholly lateral to the palatine. Here the posterior surface of the maxilla in FMNH 28350 and CM 61426 has two notches in it separated by a short spine, which helps define two channels between the maxilla and palatine. In fact, on the right side of FMNH 28350, the spine contacts the palatine and fully separates the channels. In CM 6398, 6399, 10743, and 101007, the spine is much shorter and the two channels are more or less confluent. Based on the sectioned fetus, the smaller, anteriorly directed upper channel transmits the caudal nasal nerve and sphenopalatine artery and vein, whereas the larger, anteroventrally directed lower channel transmits the major and minor palatine nerves and vessels. These represent the sphenopalatine and caudal palatine foramina, respectively (Fig. 3B). Between the upper channel and the maxillary foramen, the orbital process is riddled with small foramina in FMNH 28350 (Fig. 3A) and CM 6398, 6399, 61426, and 101007 (fewer in CM 10743), in particular nearer the latter aperture. Judging from the sectioned fetus, numerous nutrient veins occupied this area, although some foramina may have transmitted superior alveolar nerves as well.

Palatine

The palatine bones are paired, intramembranous elements contributing to the roof of the oral cavity (Figs. 1B, 2B), the floor and walls of the nasopharyngeal duct, the air passage rostral to the choanae or internal nasal aperture (visible in the fetus in Figs. 14 and 15), and the medial wall of the orbit (Fig. 3). Each palatine has horizontal and perpendicular processes, described separately below.

The horizontal processes of the palatines (Fig. 2B) form the posterior one-third of the hard palate and of the floor of the nasopharyngeal duct. They meet on the midline at the interpalatine suture that extends from opposite the back of the fifth maxillary tooth to behind the maxillary tuberosity (Figs. 9A, B, D–F); in CM 6399, the midline suture extends further posteriorly, more than one tooth length behind the maxillary tuberosity (Fig. 9C). Anteriorly, the ventral surfaces of the horizontal processes are fairly flat, but behind the sixth maxillary tooth they slope posterodorsally and are concave, except at the interpalatine suture, which bears a slight ventral keel. The keel runs the length of the interpalatine suture, but is most pronounced posteriorly. The horizontal processes meet the palatine processes of the maxilla anteriorly and laterally at an inverted *U*-shaped suture (Fig. 2B). Posterior to the maxillary tuberosity, the lateral margin of the horizontal process is angled slightly medially and meets the pterygoid bone at an oblique, posteromedially directed suture. Medial to this, the posterior margin of the horizontal process runs anteromedially to the interpalatine suture; it is uniformly thin and does not bear a postpalatine torus. The posterior margins of the right and left horizontal processes along with the paired pterygoid bones complete an inverted, irregular *U* in ventral view in FMNH 28350 (Fig. 2B). Filling in the *U* and flooring the nasopharyngeal duct above is the soft palate. The shape of the back of the palatine exhibits a continuum from a broad *U* shape to a narrow *V* shape, from FMNH 29350 to CM 6398 and 6399 to CM 61426 to CM 10743 to CM 101007 (Fig. 9).

Arranged longitudinally in the ventral surface of the horizontal process in FMNH 28350 (Figs. 1B, 2B) are 15 or so small foramina, of which four on the right and five on the left are in the palatamaxillary suture. Only the anteriormost and posteriormost foramina are somewhat symmetrically positioned. CM 6398, 6399, 61426, and 101007 have a similar arrangement, and fewer foramina are present in CM 10743. Based on the sectioned fetus, the vast majority of these foramina transmit branches of the major palatine nerve, artery, and vein as described above for the foramina on the palatine process of the maxilla. The major palatine nerve, artery, and vein enter the palatine in the orbit via the caudal palatine foramen (Fig. 3) and run forward within a palatine canal, first within the palatine and then the maxilla (visible in the fetus in Fig. 14), sending numerous branches to the hard palate. The two posteriormost foramina in the horizontal

process of the palatine in FMNH 28350 (Fig. 2B) and CM 6398 and 10743 (three in CM 61426 and 101007; in CM 6399 three on the left and four on the right) differ in that they are directed into sulci running posteriorly. In light of the sectioned fetus, these foramina, which lie posteromedial to the maxillary tuberosity, transmit the minor palatine nerve, artery, and vein to the soft palate. The minor palatine nerve and vessels run into the caudal palatine foramen posterior to the major palatine nerve and vessels and reach the palate via a separate canal (see below).

As its name indicates, the perpendicular process of the palatine (the part visible in Fig. 3) is at roughly 90 degrees to the horizontal process. In lateral view, it is visible as a small, almost *L*-shaped element in the ventral medial orbital wall. There it has broad contacts with the orbital process of the maxilla anteriorly, the orbitosphenoid dorsally, and the alisphenoid posteriorly, and narrow contacts with the orbital process of the frontal anterodorsally and the pterygoid posteroventrally. Near its posterior border, the perpendicular process has a *J*-shaped ridge (*L*-shaped on the left) that extends dorsally a short distance onto the alisphenoid. The surfaces ventral and posterior to this ridge provide attachment area for the medial and lateral pterygoid muscles, respectively, based on the sectioned fetus (both attachments are visible in the fetus in Fig. 15). In its posterodorsal corner, the perpendicular plate with the orbitosphenoid above forms the medial wall of an aperture ventral to the sphenorbital fissure (Fig. 3B). The lateral wall is formed by the alisphenoid. Based on the sectioned fetus, this aperture is the rostral opening of the pterygoid canal, which transmits the nerve of the pterygoid canal, accompanying vein, and a tiny branch of the maxillary artery. At its anterior border, the perpendicular process forms the medial wall of the sphenopalatine foramen and below that the much larger caudal palatine foramen (Fig. 3B). Visible in the floor of the caudal palatine foramen are three canals into the palatine in all specimens studied (only the posterior two are visible in Fig. 3B). From anterior to posterior, based on the fetus, these are for the major palatine nerve and vessels, a nutrient vein, and the minor palatine nerve and vessels (visible in Fig. 14). In the fetus (and presumably in the adult), the large pterygopalatine ganglion sits on the dorsal part of the palatine between the level of the optic canal and the minor palatine nerve. In addition to its exposure in the orbit, the perpendicular process forms the lateral wall of the nasopharyngeal duct at and anterior to the choanae. It contacts the pterygoid posteriorly, the pre-sphenoid posterodorsally, and the vomer anterodorsally.

Lacrima

The paired lacrimal bones are small, wedge-shaped, intramembranous elements with two major components, the facial and the orbital processes, both of which contribute to the anterior root of the zygoma (Figs. 1A–C, 2).

The boundary between these two parts is not immediately obvious. We accept the low vertical crest anterior to the lacrimal foramen as the demarcation, because it is continuous with the crest delimiting the infraorbital margin on the jugal.

The facial process of the lacrimal (Fig. 3A) is roughly rectangular, contacting the frontal dorsomedially, the maxilla anteriorly, and the jugal posterolaterally. The bulk of its surface is roughened. Dorsal to the lacrimal foramen is a rounded lacrimal tubercle (Fig. 2A), which is only slightly higher than its surroundings; this has not yet formed in CM 10473. Attached to this area in the sectioned fetus is the anterolateral margin of the orbito-auricularis muscle of Uekermann (1912) (the muscle is visible in the fetus in Fig. 15). Anteroventral and at 90 degrees to the main part of the facial process is a smooth, triangular wedge of lacrimal (Fig. 3A). Demarcating this from the remainder of the facial process is a sharp ridge continuous posterolaterally with a similarly developed ridge on the jugal bone and anteriorly with a weak ridge on the maxilla. This ridge and smooth surface on the lacrimal provide muscle attachment, as do the neighboring surfaces on the jugal and maxilla. Based on the sectioned fetus, most of this surface on the lacrimal is for the maxillonasolabialis muscle. FMNH 28350 has one tiny foramen near the anterior end of the facial process, and CM 6398, 6399, and 61426 have a half dozen or so; the facial process is covered with connective tissue in CM 101007.

Immediately posterior to the crest delimiting the facial and orbital processes in all specimens studied is an oval, posterolaterally directed lacrimal foramen (Fig. 3A), which on the right side of FMNH 28350 is split by what appears to be an osseous septum into two apertures. The lacrimal foramen is for the nasolacrimal duct and accompanying vein, based on the sectioned fetus. However, it is uncertain what went through the two openings on the right side of FMNH 28350. One possibility is that the duct and vein are in separate openings. Another is that the nasolacrimal duct has two openings, as in the Late Cretaceous eutherian *Zalambdalestes* (Wible et al. 2004). The duct is single at the lacrimal foramen on both sides in the sectioned fetus.

The orbital process of the lacrimal (Fig. 3A) is slightly smaller than the facial process. It too is roughly rectangular, though its dorsomedial edge with the frontal is irregular. The orbital process is smooth walled and, in addition to the frontal, contacts the maxilla ventrally and the jugal ventrolaterally. In FMNH 28350, there are one or two tiny foramina in the orbital process, and a small foramen between the lacrimal and frontal, between the lacrimal and maxilla, and between the lacrimal, frontal, and maxilla. The only stable one of these foramina across the remaining specimens is the last, between the lacrimal, frontal, and maxilla, the lacrimal fenestra (Fig. 3A), and it is considerably larger than the lacrimal foramen in CM 6398, 6399, 10743, 61426, and 101007. With the excep-

tion of the lacrimal fenestra, these openings likely transmitted nutritive veins, although no such apertures are present in the sectioned fetus. Passing through the lacrimal fenestra in the sectioned fetus is one of the extrinsic eyeball muscles, the inferior oblique, which originates from the back of the cartilaginous nasal capsule.

Jugal

The paired jugal bones are confined to and represent the principal elements of the zygomatic arches (Figs. 1A, B, C, 2). The jugal is a gently bowed, rod-like, intramembranous ossification. For descriptive purposes, we treat the jugal in three parts of roughly equal lengths: anteromedial, middle, and posterior. The anteromedial part overlies the zygomatic process of the maxilla, the middle part is free standing, and the posterior part underlies the zygomatic process of the squamosal. In lateral view (Figs. 1C, 2C), the anteromedial and middle parts form the arms of a broad *V*, and the posterior part is roughly horizontal.

As seen in the lateral view, the anteromedial part (Fig. 2C) is situated at the same roughly 45-degree angle to the vertical as the zygomatic process of the maxilla, which it overlies. At its medial limit, it contacts the ventral margin of the lacrimal, both its orbital and facial exposures. The anteromedial part has a distinct dorsal ridge that represents the anterior part of the infraorbital margin. The thickened, roughened anterior edge of this dorsal ridge (and the smooth walled surface on the jugal ventral to it) marks the upper limit of the attachment of the maxillonasolabialis muscle.

The middle part of the jugal extends between the zygomatic process of the maxilla anteroventrally and the zygomatic process of the squamosal posterodorsally (Figs. 2B, C). At its anterior end, the ventral margin of the jugal's middle part has a roughened process continuous with a similar surface on the zygomatic process of the maxilla described above as for the superficial masseter (Fig. 2B). Extending posteriorly from this process is a crest that runs the length of the middle and posterior parts of the jugal, but that is best developed at its anterior and posterior ends (Figs. 1B, 2B). Paralleling this crest is another one centrally located on the lateral surface of the jugal's middle part that continues onto the posterior part, along the jugal's suture with the squamosal (Figs. 1C, 2C). Based on Smith and Redford (1990, fig. 3b), these two crests and the smooth, in places concave surface between them are for the attachment of the masseter muscle. However, the sectioned fetus does not agree; the superficial masseter attaches to the ventral crest, whereas another muscle occupies the smooth surface between the ventral and dorsal crests (Fig. 14). This well-developed muscle attaches to skin in the neck and represents the zygomatic portion of the platysma of Uekermann (1912). In the fetus, the deep masseter arises from a correspon-

ding surface on the medial side of the middle and posterior parts of the jugal, but distinct crests do not indicate this in the adult.

The posterior part of the jugal has a broad contact with the zygomatic process of the squamosal (Fig. 2C). In lateral view, the suture between these two bones is essentially horizontal; the shorter medial suture is more oblique. The jugal ends posteriorly at a fairly sharp, vertical crest. It appears that this crest falls short of the glenoid fossa on the squamosal, although the limits of the glenoid are not well marked (Fig. 1B). Consequently, there appears to be no glenoid process of the jugal.

Frontal

The paired frontal bones are the major elements of the skull roof (Figs. 1A, 2A) and of the orbitotemporal region (Fig. 3A); their maximum length is more than half that of the skull. The intramembranous frontals' contributions to the skull roof and orbitotemporal region are described separately.

In dorsal view (Fig. 2A), the left and right frontals' contribution to the skull roof is roughly pentagonal. Anteriorly are two oblique sides that meet on the midline to form a *V*-shaped process inserted between the nasal bones; also contacted behind the nasals are the facial processes of the maxillae and lacrimals. Next are two concave sides, the concavities being the postorbital constriction, which define the orbital rim and include the posteromedially slanted suture with the squamosals. Posteriorly, the fifth side is the roughly horizontal suture with the paired parietal bones. The central portion of the frontal's dorsal surface is fairly flat, but the outer portion is curved downward onto the side of the face, to the orbital margin, and into the temporal fossa. Curving posteromedially from the orbital margin are weak temporal lines that continue onto the parietal. In FMNH 28350 (Fig. 2A) and CM 6398, 6399, and 61426, these lines converge anterior to the frontoparietal suture, but do not meet on the midline (Figs. 8A–D). In contrast, in CM 10743 and 101007, these lines do not converge prior to the frontoparietal, but remain near the lateral edge of the frontal's dorsal surface (Figs. 8E, F). In CM 6399, the posterior fourth of the interfrontal suture has a broad crest that extends onto the parietal where it is weakly marked. Based on the sectioned fetus, this crest provides attachment for the orbito-auricularis muscle (visible in the fetus in Fig. 14).

The orbital margin is marked by an anterolaterally directed sharp ridge on the frontal that continues onto the lacrimal (Figs. 1C, 2C). The surface of the frontal immediately medial to this ridge is roughened, as is the adjacent facial process of the lacrimal. Based on the sectioned fetus, this roughened surface and ridge on the frontal provides more attachment for the orbito-auricularis muscle. At the foramen for the frontal diploic vein (see below),

the ridge demarcating the orbital margin grades into a less distinct line that continues posteromedially as the temporal line. There is no sign of a postorbital process.

Visible in dorsal view in FMNH 28350 (Figs. 1A, 2A) are six moderate-sized foramina on the right frontal and eight on the left. In addition to number, these openings are asymmetric in position between the two sides. The anterior two foramina (three on the left) are the largest, are directed anteriorly into well-developed sulci, and are situated medial to the orbital margin. The sectioned fetus has three comparable openings that transmit an artery and vein, branches of the external ethmoidal artery and vein that arise within the cranial cavity anterior to the ethmoidal foramina and pass through the diploë of the frontal bone. Proceeding posteriorly, the next foramen is on the temporal line at the postorbital constriction and is dorsomedially directed. Its contents are the same as the anterior foramina based on the sectioned fetus. The last three foramina (four on the left) are in the temporal fossa, just anterior to the frontoparietal suture, and are anterodorsomedially directed. In the fetus, several temporal rami and accompanying veins arise from the ramus superior of the stapedial artery in the gap between the squamosal and frontal and run dorsally into the temporalis muscle. Apparently in the adult, the frontal closes the gap with the squamosal and encloses these temporal vessels in foramina. The number of foramina in the frontal varies in the other specimens (Fig. 8). Both sides of CM 10743 have five anteriorly placed foramina, only one near the midline behind that, and four in the right temporal fossa and two in the left. CM 6398 has three on the right and one on the left anteriorly, more than two dozen tiny foramina per side along the midline, and four in the right temporal fossa and three in the left. CM 6399 has four on the right and six on the left anteriorly, with one large foramen on the left near the midline behind these, as well as a number of tiny nutritive foramina on either side of the midline in this vicinity, and five in the right temporal fossa and four in the left. CM 101007 has three on the left and one on the right anteriorly, behind that are more than a dozen tiny foramina on both sides, and in the temporal fossa are three on the right and two on the left. CM 61426 has six on the right and five on the left anteriorly, more than a dozen on the skull roof behind that, and six in both temporal fossae.

In lateral view, the frontal's contribution to the orbitotemporal region is separated into two halves by a low, horizontal ridge demarcating the anteroventral margin of the temporalis muscle origin (above the anterior opening of the orbitotemporal canal in Fig. 3B). Posterodorsal to this ridge is a concave surface in the temporal fossa and anteroventral is a flat surface in the medial orbital wall. The orbital plate of the frontal forms roughly half of the medial orbital wall, and even has a slight contribution to the posterior surface of the anterior root of the zygoma, posteromedial to the lacrimal.

Anteriorly, the frontal's ventral margin contacts the orbital process of the lacrimal at an irregular suture, and behind that the orbital process of the maxilla at a suture that initially is horizontal but then slants ventrally to its lowest point dorsal to the ultimate maxillary tooth. Posterior to the maxilla, the extreme posteroventral margin of the frontal has a very narrow contact with the palatine bone and contributes to the dorsal border of the sphenopalatine foramen (Fig. 3B). Immediately above its contact with the palatine, the frontal abuts the orbitosphenoid (Fig. 3B). The suture between the frontal and orbitosphenoid runs vertically to just below the lower of the two ethmoidal foramina (see below) and then turns posteriorly to a point dorsal to the optic canal where the alisphenoid bone is met. From there, the suture between the frontal and alisphenoid curves posterodorsally to a point posterior to the anterior opening of the orbitotemporal canal (see below) where the squamosal is encountered in the ventral margin of the temporal fossa (Fig. 3B). The suture between the frontal and squamosal bends posterodorsally to the junction with the parietal on the margin of the skull roof (Fig. 3A).

Three large foramina are located within the orbital plate of the frontal near its posterior margin (Fig. 3B). The most inferior one is ventrally directed and anterodorsal to the optic foramen. It is entirely within the frontal in FMNH 28350 and CM 10743 and 6399, but between the frontal and orbitosphenoid in CM 6398, 61426, and 101007. Based on the sectioned fetus, it transmits the ethmoidal nerve, a branch of the ophthalmic nerve, the first division of the trigeminal. Dorsal and slightly anterior to this foramen is an anteroventrolaterally directed foramen that transmits the external ethmoidal artery and vein (visible in the fetus in Fig. 14) into the braincase in the fetus. A similar arrangement for the ethmoidal foramina and their contents is found in some dogs, where the openings are referred to as ventral and dorsal ethmoidal foramina (Evans 1993). Posterodorsal to the dorsal ethmoidal foramen of the yellow armadillo and connected to it by a sulcus is an anteroventrally directed foramen (Fig. 3A). In the fetus, this opening transmits the rostral continuation of the ramus superior of the stapedial artery, the ramus supraorbitalis, and companion vein into the orbit, and therefore is the anterior opening of the orbitotemporal canal (sinus canal or cranio-orbital foramen). Just ventral to the back of the ridge forming the supraorbital margin is a smaller foramen in the frontal (Fig. 3A) (double on the left side of CM 10743), which accommodates a diploic vein in the fetus. This resembles the foramen transmitting the frontal diploic vein in the dog (Evans 1993) and several other placentals (Thewissen 1989). There are several additional asymmetrically arranged foramina for diploic veins in the orbital plate in the fetus and FMNH 28350.

Parietal

The paired intramembranous parietal bones complete the roof of the posterior part of the braincase (Figs. 1A, 2A) and contribute to the temporal fossae (Figs. 1C, 2C), providing attachment for the temporalis muscle.

Each parietal is shaped roughly like a parallelogram (Fig. 2A). The slanted anterior edge contacts the frontal. The longitudinal medial and lateral edges contact the parietal of the opposite side and the squamosal, respectively. The slanted posterior edge abuts the unpaired supraoccipital and forms the anterior part of the strong nuchal (lambdoidal) crest. Most of the sutures are more or less horizontal, but parts of the suture with the squamosal are essentially at a right angle, such that the parietal is confined to the skull roof and the squamosal the sidewall (Figs. 1A, 2A). The dorsal surface of the medial half of the parietal is strongly convex, reflecting the contour of the enclosed cerebrum; the lateral half is flat and slanted somewhat ventrolaterally. The weak temporal lines present on the left and right frontals extend posteriorly onto the left and right parietals. Anteriorly on the parietal in FMNH 28350 and CM 6398, 6399, and 61426, the temporal lines converge on each other near the midline, but do not meet (Figs. 8A–C, E). Posteriorly on the parietal, in FMNH 28350, the temporal lines run parallel to each other and do not extend all the way to the nuchal crest (Fig. 2A). In contrast, in CM 6398, 6399, and 61426, they diverge posteriorly and extend to the nuchal crest (Figs. 8B, C, E). In CM 10743, the weak temporal lines are widely separated anteriorly on the parietal, run parallel to each other the length of the parietal, and do not reach the nuchal crest (Fig. 8D). Lastly, in CM 101007, the temporal lines are widely separated anteriorly on the parietal, converge posteriorly, and reach the nuchal crest (Fig. 8F). The degree of development of the temporal lines also varies in the studied sample (Fig. 8). They are very weak in FMNH 28350 and CM 10743, more raised on both the parietals and frontals in CM 6398, 6399, and 61426, and even more raised just on the parietals in CM 101007. The temporal lines mark the upper limit of the temporalis muscle origin and provide attachment for the temporal fascia (Smith and Redford 1990).

In its lateral part (Figs. 1A, 2A), each parietal is pierced by more than a dozen moderate-size, slightly asymmetrically arranged foramina; slightly fewer are present in CM 10743 (Fig. 8). Most are dorsomedially directed and some even lead into similarly oriented sulci. On the right of FMNH 28350 are eleven foramina entirely within the parietal, three in the suture with the squamosal, and one in the suture with the frontal and squamosal. On the left side of FMNH 28350 are ten within the parietal, four in the suture with squamosal, and one in the suture with the frontal and squamosal. Based on the fetus, these foramina transmit arterial and venous rami temporales from the posttemporal and orbitotemporal

canals (see Fig. 17). Nearer the midline, in FMNH 28350, medial to the temporal lines, each parietal has about ten minute foramina, which likely are parietal foramina transmitting emissary veins (Figs. 1A, 2A).

Pterygoid

The paired pterygoid bones are roughly vertical elements that lie beneath the sphenoid complex in the mesocranium and are the major components of the entopterygoid crests, which form the lateral walls of the basipharyngeal canal, the bony roof of the nasopharynx posterior to the choanae (Figs. 1B, 2B). The pterygoids are laminar, thinner in the middle and thickened along both the dorsal and ventral edges. In therian mammals, the pterygoid bones form from two embryonic components, a dorsal intramembranous part and a ventral cartilaginous part, that fuse together (Presley and Steel 1978). The sectioned fetus probably conforms to this pattern as its pterygoid preserves cartilage in its ventralmost extent (Fig. 15). We describe the adult pterygoid in lateral and medial views.

In lateral view (Fig. 3), the pterygoid is roughly a right triangle, with the 90-degree angle situated posteroventrally. Its ventral side does not contact bone. Its posterior side is the shortest and most of it also does not contact bone. Its oblique side opposite the 90-degree angle contacts the alisphenoid through most of its length and the perpendicular plate of the palatine anteriorly. In the fetus, two muscles have attachment to the lateral surface of the pterygoid: the medial pterygoid anteriorly and the tensor veli palatini posteriorly. In the adult, the pterygoid has a muscular scar continuous anteriorly with the medial pterygoid fossa on the perpendicular process of the palatine and alisphenoid, and an obliquely oriented, oval fossa posterodorsally, presumably for the tensor of the soft palate. Posteroventrally, at the right angle on the pterygoid is a robust, triangular hamular process that is directed ventrally and slightly posteriorly (Fig. 3). Three muscles are associated with the hamulus in the fetus. Attached to the posterior surface is the superior pharyngeal constrictor; running across the posterior surface dorsal to the superior constrictor is the levator veli palatini; and running across the ventral surface is the tensor veli palatini. Another process extends dorsolaterally from the posterodorsal corner of the pterygoid toward the ear region. This narrow process contacts the auditory bulla and, therefore, is identified as a tympanic process of the pterygoid (Figs. 3, 5C).

The composition of the lateral wall of the basipharyngeal canal differs in the specimens studied. In FMNH 28350 and CM 10743, the pterygoid in medial view is significantly larger than it is in lateral view. It is roughly a square, with the narrow tympanic process extending from the posterodorsal corner. Anteriorly, the pterygoid has an irregular suture with the palatine: the horizontal

process ventrally and the perpendicular process dorsally. Dorsally, it contacts the basisphenoid, except anteriorly where it has a small contact with the presphenoid (Fig. 2B). In contrast, in CM 6399, 61426, and 101007, the pterygoid in medial view has roughly the same profile (size and shape) as it does in lateral view. Its anterodorsal margin contacts the palatine, but its anterodorsal margin contacts a separate, wedge-shaped bone interposed between the palatine and pterygoid that is fused seamlessly with, but lies at a right angle to, the basisphenoid. We interpret this bone as the medial surface of the alisphenoid; the fetus studied by us is not advanced enough to ascertain whether this belongs to the ali- or basisphenoid ossification. CM 6398 is intermediate between the two extremes. A small wedge of alisphenoid is present, but overlying the two ventral sides of the wedge is the pterygoid.

The most conspicuous feature on the pterygoid's medial surface, including the tympanic process, is the passageway for the nerve of the pterygoid canal, which differs among the specimens studied. On the left side of FMNH 28350, a narrow, longitudinal groove begins posteriorly on the tympanic process and runs forward near the dorsal margin. This groove disappears into a small foramen within the pterygoid situated posteroventral to the presphenoid-basisphenoid suture. On the right side of FMNH 28350, a short segment of the groove is enclosed as a canal at the posterodorsal corner of the pterygoid (Figs. 4A, B). CM 10743 resembles the right side of FMNH 28350 except that the groove disappears from the basipharyngeal canal via a foramen between the pterygoid and palatine, and not within the pterygoid. In CM 61426, the groove on the pterygoid is open on the right and enclosed on the left, with CM 101007 showing the opposite pattern. In these two specimens, the pterygoid canal structures have a short course on the medial side of the pterygoid, but rostral to that a very long course in a groove on the medial side of the alisphenoid prior to their exit from the basipharyngeal canal between the alisphenoid and palatine. In CM 6398 and 6399, there is a canal within the pterygoid posteriorly and then an open groove on the alisphenoid, which disappears into a foramen between the pterygoid and alisphenoid in the former and between the alisphenoid and palatine in the latter. Based on the fetus, the major occupant of these various grooves and canals is the nerve of the pterygoid canal, with very small accompanying artery (arising from the maxillary artery) and vein. In the fetus, these structures make their way into the cavum epiptericum, the extradural space within the cranial cavity for the trigeminal ganglion (Gaupp 1908), via an aperture between the pterygoid, the perpendicular process of the palatine, the basisphenoid, and the alisphenoid, and then ultimately into the orbit. Near the posterior margin of the pterygoid in the FMNH 28350, ventral to the groove for the pterygoid nerve are several small foramina asymmetrically placed between

the right and left side. In light of the sectioned fetus, these are nutrient foramina.

Ethmoid

Broom (1926, 1927, 1935) observed that some mammals have a separate mesethmoid ossification (=ethmoid of this report), whereas in others the corresponding area of the nasal cartilages ossifies as part of the presphenoid. As a consequence, the number of bones on the mammalian basicranial axis varies between three (presphenoid, basisphenoid, and basioccipital) and four (these three plus the mesethmoid). Broom (1927, 1935) subdivided mammals into the Palaeotherida, taxa without the mesethmoid, and Neotherida, taxa with the mesethmoid. Based on observations of *Dasypus* sp. (= *Tatusia* sp.), *Cyclopes* sp. (= *Cycloturus* sp.), and *Choloepus didactylus*, Broom included Xenarthra in the Palaeotherida along with monotremes, marsupials, golden moles, and some ungulates. Broom's conclusions were embraced by De Beer (1937) in his very influential treatise on the development of the vertebrate skull and continue to be cited by more recent authors (e.g., Zeller 1989; Clark and Smith 1993; Wible 2003).

The sectioned yellow armadillo fetus available to us provides no information relevant to this problem, because only two midline ossifications are present, the basioccipital and basisphenoid, along with the paired orbitosphenoid ossifications (the last is visible in Fig. 11). However, a report by Ferigolo (1981) on two skulls of young *Euphractus sexcinctus*, both 70 mm in length, is relevant. In one specimen, the left and right orbitosphenoid ossifications are separated by cartilage from each other and from ossification centers in the middle portion of the cribriform plate and in the perpendicular plate of the ethmoid. In the second specimen, the left and right orbitosphenoids are fused seamlessly, without a separate presphenoid ossification, and the middle portion of the cribriform plate and adjacent perpendicular plate has a single ossification center. Ferigolo (1981) concluded that four bones are present on the basicranial axis of the yellow armadillo: mesethmoid, orbitosphenoid, basisphenoid, and basioccipital. He further suggested that the xenarthran specimens studied by Broom (1927, 1935) were too advanced to justify his conclusions in that the mesethmoid and orbitosphenoid ossifications already had fused into one element. Ferigolo's study raises serious doubts about the reality of the morphological basis for Palaeotherida and Neotherida and awaits further study in more, relevant taxa. The apparent absence of a presphenoid ossification in the yellow armadillo is yet another example of the variability in the formation of this part of the skull. The presphenoid has been reported to have two centers of ossification (e.g., *Elephantulus*, Roux 1947; *Canis*, Evans 1993), one center of ossification (e.g., *Monodelphis*, Clark and Smith 1993), or no separate cen-

ter, with the orbitosphenoids fusing on the midline (e.g., *Suncus*, Roux 1947; *Dasypus*, Reinbach 1952b; *Manis*, Jollie 1968).

The fate of these various ossification centers cannot be studied in the adult yellow armadillos available to us, because the potential sutures are obscured by overlying bones. We do not know whether the orbitosphenoids are fused seamlessly at the midline, as observed in young yellow armadillos by Ferigolo (1981), or whether the mesethmoid and orbitosphenoids also are fused seamlessly, as Ferigolo (1981) believed to be the case in the *Dasypus* sp. studied by Broom (1927). Nevertheless, following Ferigolo (1981), we accept that a mesethmoid (=ethmoid) is present in the yellow armadillo. However, we do not describe this element here, because it is hidden completely beneath other cranial bones in the adult and we do not know the limits of this element with regard to the nasal cartilages of the sectioned fetus. The cross sections of the fetal armadillo in Figures 11–13 illustrate some features of the nasal cartilages. For descriptions and illustrations of the nasal cartilages in other prenatal armadillos, we refer the reader to studies on *Dasypus* (Reinbach 1952a, 1952b; Werner 1960) and *Zaedyus* (Reinbach 1955).

Vomer

The unpaired vomer is the longest cranial bone in the yellow armadillo, being more than half the length of the skull. This intramembranous element is confined entirely to the nasal cavity, but some features are visible through the external and internal nasal apertures.

In FMNH 28350, at the external nasal aperture, the vomer is visible as a narrow, longitudinal rod, *V*-shaped in cross section, lying dorsal to the premaxilla and maxilla and with the cartilaginous nasal septum lodged within the *V*. Based on the sectioned fetus, sitting ventrolateral to the arms of the *V* are the vomeronasal cartilages, which extend from a level in front of the premaxillary tooth germ to the gap between the second and third maxillary tooth germs (Fig. 12). At the posterior end of the vomeronasal cartilages, these elements are surrounded (invaded) by the vomer ossification (Fig. 13), as has been described for some other placentals (e.g., *Zaedyus*, Reinbach 1955; *Manis*, Jollie 1968; *Elephantulus*, Roux 1947).

At the choanae, the right and left alae of the vomer taper posteriorly to a sharp point that falls just short of the choanae. The origin of the alae from the vomer appears to lie roughly dorsal to the palatomaxillary suture on the hard palate. The alae underlie the presphenoid and posterolaterally contact the palatines. It could not be determined if the alae contact the maxillae anterior to the palatines.

Sphenoid Complex

In the sectioned fetus, the chondrocranium in front of the ear region has five separate ossification centers: one on the midline below the hypophysis that represents the basisphenoid; paired centers lateral to the basisphenoid, associated with the mandibular nerves, that represent the alisphenoids; and paired centers anterior to the alisphenoid, associated with the optic nerves, that represent the orbitosphenoids. There is neither a presphenoid ossification between the orbitosphenoids nor an ethmoid ossification more anteriorly (see ethmoid above). The nasal cartilages are unossified with the exception of the posterior part of the vomeronasal cartilage, which as stated above is surrounded by the vomer ossification (Fig. 13). It is unclear how many separate bones result from this complex in the adult. The pterygoid bones underlie the predicted juncture of the basisphenoid and the alisphenoids in the two specimens that preserve the most sutural information, CM 10743 and FMNH 28350 (Fig. 2B), obscuring the view of any potential suture. What we interpret is the basisphenoid and alisphenoid juncture is visible in the basipharyngeal canal in CM 6398, 6399, 61426, and 101007 and no suture is present; however, these specimens have fused sutures that are open in CM 10743 and FMNH 28350 (e.g., between the basisphenoid and basioccipital). Nevertheless, we deem it likely that the basisphenoid and the alisphenoids are fused in the yellow armadillo. For descriptive purposes, we identify the basisphenoid as the bone in the skull base medial to the pterygoids and the alisphenoids as the bones in the orbitotemporal fossa lateral to the pterygoids (Fig. 2B) and anterior to the pterygoids in the basipharyngeal canal in CM 6398, 6399, 61426, and 101007. The palatine bones underlie the predicted juncture of the orbitosphenoids with a midline presphenoid. As stated above, in two young yellow armadillos, both with skulls 70 mm in length, Ferigolo (1981) found the orbitosphenoids to be fused on the midline without a presphenoid ossification. We can neither confirm nor deny this observation. However, for descriptive purposes, we identify the midline element in the basipharyngeal canal anterior to the basisphenoid as the presphenoid (Fig. 2B) and the lateral elements in the orbit as the orbitosphenoids (Fig. 3). FMNH 28350 and CM 10743 preserve sutures that delimit the presphenoid and the basisphenoid, as well as the basisphenoid and the basioccipital (Figs. 2B, 9A, D). In contrast, in CM 6398, 6399, 61426, and 101007, these sutures are obliterated and there is only a single bone on the basicranial axis (Figs. 9B, C, E, F).

Presphenoid

As mentioned above, we identify the presphenoid as the midline ossification on the basicranial axis anterior to the basisphenoid and medial to the palatines. We describe the

presphenoid based on FMNH 28350 and CM 10743, the only specimens to preserve the presphenoid-basisphenoid suture (Figs. 2B, 9A, D). In ventral view (Figs. 1B, 2B), only the posteriormost part of the presphenoid is visible where it forms the flat roof of the choanae. The posterior border of the presphenoid, which contacts the basisphenoid, is concave. Just within the choanae, the posterolateral border of the presphenoid has a narrow contact with the pterygoid (visible in ventral view) and then anterior to that the palatine in FMNH 28350; it contacts only palatine in CM 10743. From the level of the maxillary tuberosity to the horizontal palatamaxillary suture, the presphenoid is underlain by the alae of the vomer within the nasopharyngeal duct. As the alae converge anteriorly on the body of the vomer, the rod-shaped ventral surface of the presphenoid tapers as well. The anterior extent of the presphenoid cannot be determined as it is hidden by the vomer.

Orbitosphenoid

The visible part of the paired orbitosphenoids is confined to the medial orbital wall, where it has a small exposure (Fig. 3). The orbitosphenoid is roughly quadrangular, slightly longer than deep, and deeper anteriorly than posteriorly (Fig. 3B). It contacts the frontal anteriorly, the frontal and alisphenoid dorsally, the alisphenoid posteriorly, and the perpendicular plate of the palatine ventrally. The anterodorsal corner of the orbitosphenoid approximates but does not contribute to the ventral ethmoidal foramen in FMNH 28350 and CM 6399 and 10743. However, the ventral ethmoidal foramen is between the orbitosphenoid and frontal in CM 6398, 61426, and 101007. Ventral to this are three or four tiny foramina of uncertain function in the suture between the orbitosphenoid and frontal. The most salient feature on the orbitosphenoid is the optic canal, which is centrally positioned along the length of the bone, but close to the dorsal border. The optic canal is circular and anterolaterally and slightly ventrally directed. Based on the sectioned fetus, in addition to the optic nerve, the optic canal transmits an ophthalmic artery and accompanying vein (Fig. 15); the ophthalmic artery is derived from the cerebral circulation and within the orbit anastomoses with the ramus orbitalis, a branch of the ramus supraorbitalis. Ventral and anterior to the optic canal is a short, near horizontal ridge on the left orbitosphenoid of FMNH 28350 (bilateral in CM 6398, 6399, 61426, and 101007) that is barely perceptible on the right side of FMNH 28350 (bilateral in CM 10743). We interpret this ridge as the ossified ala hypochiasmatica (Fig. 3B), a process of the orbital cartilages that provides attachment for the extraocular eye muscles other than the levator palpebrae superioris and obliquus inferior in the sectioned fetus and in prenatal *Dasypus* (Reinbach 1952a) and *Zaedyus* (Reinbach 1955). Dorsal and anterior to the optic canal in

CM 6398 and 6399 is a low ridge, more pronounced on the right side, that extends anterodorsally a short distance onto the frontal to the ventral ethmoidal foramen. The posterior margin of the orbitosphenoid contributes to the walls of two openings (Fig. 3B). Dorsally, between the orbitosphenoid medially and alisphenoid laterally is the well-developed sphenorbital fissure, which in the sectioned fetus transmits the oculomotor, trochlear, abducens, ophthalmic, and maxillary nerves, accompanying veins, and a tiny branch of the maxillary artery. Ventrally, between the orbitosphenoid and palatine medially and the alisphenoid laterally is the smaller rostral opening of the pterygoid canal.

Basisphenoid

As mentioned above, we identify the basisphenoid as the midline ossification on the basicranial axis anterior to the basioccipital and medial to the pterygoids (Figs. 1B, 2B). We describe the basisphenoid based on FMNH 28350 and CM 10743, the only specimens to preserve the sutures delimiting the basisphenoid from the presphenoid and basioccipital (Figs. 9A, D). The basisphenoid is a flat, roughly trapezoidal element that forms most of the roof of the basipharyngeal canal. Its anterior and posterior sides are generally convex, abutting the presphenoid and the basioccipital, respectively; its lateral sides are concave, underlain by the pterygoid bones. It is widest posteriorly, and there it is as wide as it is long. On the midline in FMNH 28350 (Figs. 2B, 9A), nearer the anterior border than the posterior, is a small opening into the cranial cavity, the craniopharyngeal canal, which in the sectioned fetus transmits a remnant of Rathke's pouch, and accompanying vein. In CM 6399, 10743, 61426, and 101007, this canal is present, but reduced in size; CM 6398 has two canals, anterior and posterior to each other (Figs. 9B–F). In FMNH 28350, there are two tiny foramina anterior to the craniopharyngeal canal and one posterior, all of uncertain function (Fig. 2B). At the posterolateral border of the basisphenoid is the carotid foramen, which has a complex structure (Fig. 4). The foramen principally lies between the basisphenoid and the anterior pole of the promontorium of the petrosal, with each element roughly an equal contributor. However, underlying and obscuring the anterior pole of the promontorium is the entotympanic. In addition, in CM 6399 and 101007, underlying and obscuring part of the basisphenoid is the tympanic process of the pterygoid; this element does not reach the carotid foramen in FMNH 28350 (Fig. 4C) and CM 6398, 10743, and 61426. In the sectioned fetus, the carotid foramen transmits the internal carotid artery and vein, along with some but not all of the internal carotid nerve. Part of the internal carotid nerve enters the cranial cavity lateral to the aliochlear commissure, the cartilaginous bar that forms the lateral wall of the carotid foramen, and medial to the alisphenoid. We cannot determine

whether such an aperture is preserved in FMNH 28350 because this region is obscured by the auditory bulla, the tympanic process of the pterygoid, and some preserved dried tissue. However, in CM 61426, it can be seen that the lateral wall of the carotid foramen is not entirely closed; a narrow gap between the basisphenoid and petrosal is continuous with a wider lateral gap, the equivalent of a piriform fenestra (MacPhee 1981). In other armadillos, such as *Dasypus kappleri* CM 76828, a sizeable gap separates the promontorium from the alisphenoid and the basisphenoid anteriorly and the basioccipital medially; included in this gap are the piriform fenestra anterolaterally, the carotid foramen anteromedially, the foramen for the inferior petrosal sinus medially, and the jugular foramen posteromedially.

Alisphenoid

The paired alisphenoids contribute to the orbitotemporal fossa (Fig. 3) and the basicranium (Fig. 4), and the basipharyngeal canal in CM 6398, 6399, 61426, and 101007 (see pterygoid above). In lateral view (Fig. 3), the alisphenoid is roughly triangular, with straight, obliquely oriented posteroventral and posterodorsal sides and a very irregular, more or less vertical anterior side. The main contact of the posteroventral side is with the pterygoid, where the alisphenoid forms the lateral side of the base of the entopterygoid crest; the posteroventral side has a small contact with the auditory bulla at the posteriormost extreme. The entire posterodorsal side abuts the squamosal, anteroventral to the squamosal's zygomatic process. The anterior side, from dorsal to ventral, contacts the frontal, orbitosphenoid, and palatine. The contact with the frontal is broad and convex, and that with the palatine is broad and irregular. However, the contact with the orbitosphenoid is only at the dorsal and ventral margins of that bone. In between these narrow contacts, the anterior margin of the alisphenoid is concave and forms the lateral wall of the well-developed sphenorbital fissure, the orbitosphenoid forming the medial wall (Fig. 3B). Ventral to this, there is a second concavity in the anterior margin of the alisphenoid where the alisphenoid is separated from the orbitosphenoid and palatine, and forms the lateral wall of the rostral opening of the pterygoid canal (Fig. 3B). The posterior margin of the alisphenoid has a low ridge that runs from the posterolateral base of the entopterygoid crest to the entoglenoid process of the squamosal. Because the posterodorsal face of this ridge abuts the auditory bulla, we identify the ridge as a tympanic process of the alisphenoid (Fig. 4C). Anterior to this ridge is a large, ovoid depression that leads into two subequal foramina (Fig. 3B). The larger, dorsal, ventrally directed opening is the foramen ovale, which in the sectioned fetus transmits the mandibular nerve, accompanying small vein, and a small meningeal branch of the maxillary artery. The smaller, ventral, anterolaterally directed

foramen is the transverse canal foramen, which in the sectioned fetus transmits a large vein from the cavernous sinus. It is unclear in the adult whether the right and left transverse canals communicate across the midline within the basisphenoid, as in some marsupials (Sánchez-Villagra and Wible 2002); in the sectioned fetus, they do not. Two muscles of mastication attach to the alisphenoid in the sectioned fetus. The lateral pterygoid attaches anterodorsal to the foramen ovale and transverse canal foramen (Fig. 15), whereas the medial pterygoid is anteroventral to these openings.

Squamosal

The paired squamosals are intramembranous bones that contribute to the side wall of the braincase, the posterior zygoma, and the middle ear, and house the cranial part of the temporomandibular joint (Figs. 1A, C; 2A, C; 3A; 4A, B).

In lateral view (Fig. 3A), the squamosal, without the zygomatic process, is roughly pentagonal. The five sides of the pentagon are as follows: anterodorsally, the oblique suture with the frontal; posterodorsally, the longitudinal suture with the parietal; posteriorly, the oblique suture with the supraoccipital and the mastoid exposure of the petrosal; posteroventrally, the oblique suture with the auditory bulla; and anteroventrally, the oblique suture with the alisphenoid. The zygomatic process of the squamosal divides the squamosal into a larger dorsal squamous part in the lateral braincase wall and a ventral part in the basicranium (Figs. 2C, 3A). The squamous part provides attachment for the temporalis muscle (Smith and Redford 1990, fig. 3b) and is pierced by numerous moderate- to small-size foramina, asymmetrically arranged between the right and left sides. In FMNH 28350, anterior to the posterior root of the zygomatic process, there are five foramina on the left side (Fig. 3A) and three on the right plus two between the squamosal and parietal; both sides have an additional foramen at the juncture of the squamosal, parietal, and frontal. Posterior to the posterior root of the zygomatic process in FMNH 28350, there are four foramina on both sides (Fig. 3A) plus an additional foramen between the squamosal and parietal on the right. Two foramina are constant between the right and left sides. The more anterior of these is not visible in lateral view, because it is hidden by the posterior root of the zygomatic process; in dorsal view (Fig. 2A), it lies opposite the anterior margin of the external acoustic meatus. The more posterior one is positioned dorsolateral to the external acoustic meatus and below the suprameatal bridge, the crest that is continuous anteriorly with the dorsal margin of the zygomatic process; on the left side the external surface of this foramen has a narrow bony bridge that delimits a small dorsal opening from a large ventral opening (Fig. 3A). Foramina in the squamous part of the squamosal or near its suture with the

parietal occur in many mammals (Cope 1880; Cartmill and MacPhee 1980) and have been called by a variety of names. We follow Wible (2003) and Wible et al. (2004) in identifying the foramen below the suprameatal bridge as a suprameatal foramen (Fig. 3A) and the remaining openings as subsquamosal foramina. Based on the sectioned fetus, these foramina transmit rami temporales of the stapedia artery system and accompanying veins (see below). The posterior edge of the squamous part, which abuts the supraoccipital and the petrosal, is thickened and forms the ventrolateral part of the nuchal crest (Fig. 2C).

The number and position of the foramina in the squamous part of the squamosal differs in the studied specimens. Anterior to the posterior root of the zygomatic process on each side of CM 6398 are nine in the squamosal plus three between the squamosal and parietal. In CM 6399 are five on the right plus two between the squamosal and parietal and eleven on the left plus four between the squamosal and parietal. In CM 10743, there are eight on the right plus three between the squamosal and parietal, and six on the left plus five between the squamosal and parietal. In CM 61426, both sides have three within the squamosal and three between the squamosal and parietal. In CM 101007, both sides have three within the squamosal plus two between the squamosal and parietal. Posterior to the posterior root of the zygomatic process, in CM 6398 are a suprameatal foramen plus three others on the left and one on the right; both sides also have three between the squamosal and parietal. In CM 6399 are a suprameatal foramen on the right side only, with four other small foramina on both sides, one of which is between the squamosal and parietal. In CM 10743 are a suprameatal foramen plus three others on both sides, in CM 61426 are a suprameatal foramen plus five others on the right and seven on the left, and in CM 101007 are a suprameatal plus two on the right and one on the left.

In the sectioned fetus, the squamous part of the squamosal contributes to the lateral wall of a large, longitudinal vascular canal that runs between the occiput and the orbit; the medial wall is formed by the cartilaginous auditory capsule posteriorly (Fig. 17) and anteriorly by the lamina parietalis (Fig. 16), a dorsal extension of the auditory capsule. The primary occupant of this canal is an artery that arises from the occipital artery posteriorly and ends in the orbit, at an aperture wholly within the frontal in the adult, where it distributes branches with the ophthalmic nerve. For descriptive purposes, this canal is divided into anterior and posterior parts, the orbitotemporal and posttemporal canals, respectively, because the arterial occupants of each part represent the anterior and posterior divisions of the ramus superior of the stapedia artery (Wible 1987; Rougier et al. 1992). The fetal yellow armadillo preserves a tiny remnant of the intratympanic stapedia artery with its primary branches, the ramus superior and ramus inferior (the latter is visible in the

tegmen tympani in Fig. 16). The ramus superior runs dorsally through the tympanic roof and enters the longitudinal canal at the level of the postglenoid foramen in the squamosal. Consequently, the longitudinal canal anterior to this point is the orbitotemporal canal, containing the rostral continuation of the ramus superior and accompanying small vein (Fig. 16), and the longitudinal canal posterior to this point is the posttemporal canal, containing the arteria diploëtica magna and an accompanying large vena diploëtica magna (Fig. 17). As these vessels are within their respective canals, they send off arterial and venous rami temporales that penetrate the sidewall of the braincase to supply the temporalis muscle. We are not entirely certain how the fetal arrangement translates to the adult skull, but we think that the foramina in the squamous part of the squamosal anterior to the zygomatic root are derived from the orbitotemporal canal, whereas those posterior to the zygomatic root are derived from the posttemporal canal. As described below, the suprameatal foramen communicates with the postglenoid foramen; we think that it likely also communicates with the posttemporal canal.

The zygomatic process of the squamosal contributes to the posterior half of the zygoma (Fig. 2C). The anterior half of the zygomatic process overlies the jugal bone; the posterior half bends posteromedially and merges with the main part of the squamosal on the braincase wall (Fig. 2A). The lateral surface of the zygomatic process is roughened by numerous minute to tiny grooves and foramina (Fig. 1C). In FMNH 28350, there is one small, anteriorly directed foramen in the lateral surface dorsal to the front edge of the external acoustic meatus (Fig. 2C); this is double in CM 10743 and absent in CM 6398, 6399, 61426, and 101007. It opens medially on the basian surface just anterolateral to the postglenoid foramen and presumably transmits a tributary of the capsuloparietal emissary vein (postglenoid vein). The medial surface of the zygomatic process is smooth and is continuous posteromedially with the smooth-walled squamous part of the squamosal. These surfaces provide attachment for the temporalis muscle. On the right side of FMNH 28350 (and bilaterally in the remaining specimens), there is a small, anteriorly directed foramen where the medial surface of the zygomatic process and the squama meet (Fig. 2A); this is likely continuous with the orbitotemporal canal. The dorsal margin of the zygomatic process has a well-developed crest (Fig. 2A) that continues posteriorly as the suprameatal bridge (Fig. 3A) mentioned above. This crest presumably marks the lateral limit of the origin of the temporalis muscle.

The bulk of the squamosal surface visible in ventral view (Figs. 1B, 2B) represents the glenoid fossa. The glenoid's articular surface is only demarcated on its posterior border and there, by a low ridge. The articular surface is shaped roughly like an oblique teardrop with the point of the drop on the zygomatic process (Figs. 4A, B).

Overall, the glenoid fossa is gently convex. The part of the articular surface on the zygomatic process is essentially flat and more ventral than the medial part of the fossa, with the main convexity between the two. Posterior to the glenoid fossa is a deep recess entirely within the squamosal (not visible in the direct ventral view in Fig. 2C, but visible in the oblique ventral view in Figs. 4A, B). In FMNH 28350, in the posteriormost extent of this recess, dorsal to the external acoustic meatus, there is a large, anteriorly directed postglenoid foramen (single on the right, trifurcated on the left), which based on the fetus transmits the capsuloparietal emissary vein from the skull. In CM 10743, it is single on the left, trifurcated on the right; and in CM 6398, 6399, 61426, and 101007, it is single bilaterally. Anterolateral and posterolateral to the postglenoid foramen in FMNH 28350 are smaller apertures; the former connects with the small foramen on the lateral surface of the zygomatic process and we think the latter connects with the suprameatal foramen. These foramina are absent in CM 6398, 6399, and 61426, but the posterolateral one is present on the left side of CM 10743 and on both sides of CM 101007.

Posterior and medial to the glenoid fossa and postglenoid foramen are well-developed, steep processes on the squamosal that in FMNH 28350 are fused seamlessly with the auditory bulla except at the anteromedial extreme. Fortunately, the relevant sutures are preserved in CM 10743. This specimen reveals that there are really two processes on the squamosal separated by the anterior crus of the ectotympanic. The larger posterolateral process, the postglenoid process, forms the anterolateral face of the external acoustic meatus (Figs. 3A, 4A, B). (Patterson et al. 1989 reported that the postglenoid process is lacking in xenarthrans with the exception of the Eocene armadillo *Utaetus buccatus*.) The postglenoid process's position behind the postglenoid foramen is unusual but not unique; it occurs, for example, in Late Cretaceous zalamdalestids and asioryctitheres (Wible et al. 2004). The anteromedial process, the entoglenoid process, is continuous with the much weaker tympanic process of the alisphenoid described above (Fig. 4). Projecting between the entoglenoid process and the ectotympanic is the club-shaped end of the anterior process of the malleus. Medial to the anterior process of the malleus is a narrow aperture that based on the sectioned fetus transmits the chorda tympani nerve and, therefore, is a Glaserian fissure (Figs. 4A, B). Behind the postglenoid process, the squamosal forms most of the roof and makes a small contribution to the posterior wall of the external acoustic meatus based on CM 10743 (see ectotympanic below). The small contribution to the posterior wall represents the posttympanic process of the squamosal (Fig. 3A).

The open right auditory bulla reveals the presence of a large epitympanic sinus (visible in Fig. 4 is the nar-

row ventral opening into the sinus), previously noted by Kampen (1905) and Patterson et al. (1989). An epitympanic sinus (sensu Klaauw 1931) is an accessory diverticulum dorsal to the tympanic cavity proper. We describe the connection between the epitympanic sinus and the tympanic cavity proper elsewhere (see petrosal below). Here we repeat the description of the cuphractine epitympanic sinus from Patterson et al. (1989: 21). "The recessus epitympanicus [housing the mallear-incudal articulation] passes directly into a large epitympanic sinus, which extends anteriorly beneath the posterior part of the recess behind the glenoid articulation and posteriorly into the pars mastoidea [of the petrosal]. In the young specimen of *Chaetophractus* already referred to [FMNH 63865], it is partially divided by a horizontal septum into two portions, of which the lower, and smaller, appears to correspond in part to the posterior evagination of the recessus epitympanicus seen in *Cabassous* and *Tolypeutes*. Van Kampen noted the presence of an epitympanic sinus in *Euphractus* and *Zaedyus* [Zaedyus] but was uncertain as to whether it lay wholly in the squamosal. Our material shows that it is bounded medially by the periotic [petrosal]." Our observations on FMNH 28350 agree with this with one exception. There appears to be a very thin septum within the epitympanic sinus. Rather than horizontal, it is vertical and obliquely oriented, extending from the level of the fossa incudis behind the epitympanic recess medially and the postglenoid foramen laterally. The septum separates anteromedial and posterolateral chambers within the epitympanic sinus, with the former connected to the epitympanic recess. A large round opening in the medioventral part of the septum connects the two chambers. It is uncertain whether the septum is formed by squamosal, petrosal, or both. The sectioned fetus is of no use in understanding the adult anatomy of the epitympanic sinus, because this diverticulum has not yet formed.

Petrosal

The paired petrosals are the endochondral bones that house the organs of hearing and equilibration. Two divisions of the petrosal are generally recognized: the pars cochlearis, enclosing the cochlear duct and the saccule of the inner ear, and the pars canicularis, enclosing the utricle and the semicircular canals. The therian petrosal presents four surfaces (MacIntyre 1972; Wible 1990): tympanic or ventral, cerebellar or dorsal, squamosal or lateral, and lambdoid or mastoid. In FMNH 28350, the cerebellar, squamosal, and left tympanic surfaces are not available for study. On the right side (Fig. 4), part of the auditory bulla has been removed, exposing part of the tympanic surface. Consequently, our descriptions below are limited to the area of the right tympanic surface that is not hidden by the remaining auditory bulla and both mastoid surfaces (Figs. 2B, 5).

Tympanic View (Fig. 4).—In direct ventral view, three principal spaces of the middle ear are visible. The large medial space bordering the promontorium of the petrosal or cochlear housing is the tympanic cavity proper. Lateral to the tympanic cavity proper are dorsal and ventral spaces: the epitympanic sinus and the external acoustic meatus, respectively. The epitympanic sinus has been described above (see squamosal). The cylindrical external acoustic meatus is formed principally by the ectotympanic bone and will be discussed more fully with that element (see auditory bulla and ectotympanic). Separating the epitympanic sinus and the external acoustic meatus is the bony roof of the external acoustic meatus, which is formed by the ectotympanic and the squamosal based on CM 10743. A large aperture lying in two planes connects the tympanic cavity proper and the epitympanic sinus (Fig. 4C): a horizontal ventrolateral plane and a vertical dorsomedial plane; the tympanic membrane and the external acoustic meatus lie entirely lateral to this aperture. Part of the ventrolateral edge of this aperture is irregular and appears to have been damaged, because a segment of the ectotympanic's crista tympanica for the attachment of the tympanic membrane is missing.

The most salient feature in the tympanic cavity proper is the ovoid promontorium of the petrosal, the main part of the pars cochlearis, which has no vascular or nervous sulci (Fig. 4). We were not able to ascertain the number of coils for the cochlea in the sectioned fetus, but two and a half are reported in adult *Dasypus septemcinctus* (Kawano 1924). Extending from the anterior and anteromedial surface of the promontorium is an extensive epitympanic wing (Fig. 4C). The epitympanic wing is not flat, but angled at roughly 45 degrees to the skull base such that it is more ventral medially. Along its periphery, the epitympanic wing is underlain by the auditory bulla, here formed by the entotympanic (see auditory bulla below). Although partially obscured by the bulla, it is apparent that the epitympanic wing bears a sizeable facet for the bulla medially; whether a similar facet occurs anteriorly cannot be determined. There are two tiny foramina between the epitympanic wing and the auditory bulla: one at the anteromedial corner and a second one slightly lateral to that (Fig. 4C). Extending posterolaterally from these foramina a short distance on the ventral surface of the epitympanic wing are faint sulci. Based on the sectioned fetus, the most likely occupants of these foramina and sulci are veins draining into the cavernous sinus either via the carotid foramen or the piriform fenestra. Other potential occupants (e.g., greater and lesser petrosal nerves) are more laterally placed.

In the posterior and posterolateral surfaces of the promontorium are two large, subequal openings, the fenestra cochleae (round window) and fenestra vestibuli (oval window), respectively (Fig. 4C). The fenestra cochleae, which is covered by the secondary tympanic

membrane in life, is recessed slightly from the promontorial surface, producing a cochlear fossula. This recession along with the retained part of the posterior bullar wall make it difficult to obtain a full view of the fenestra cochleae. The fenestra cochleae appears to be ovoid; Ardouin (1937) reported it to be slightly wider than high in the yellow armadillo. The fenestra vestibuli, which accommodates the footplate of the stapes in life, is also recessed within a shallow pit that is deepest posteromedially, the vestibular fossula. The fenestra vestibuli is directed ventrolaterally and slightly posteriorly and is much longer than wide with a stapedial ratio (of Segall 1970, length/width) of 2.0; it is 1.92 based on the dimensions of the fenestra vestibuli published in Ardouin (1937). There is a raised lip around the circumference of the fenestra vestibuli that is slightly irregular, in particular anteriorly. Separating the fenestra cochleae and vestibuli is a narrow, vertical crista interfenestralis (Fig. 4C). As noted by Ardouin (1937), there is a small process on the lateral edge of the crista interfenestralis. Based on Ardouin's illustration (1937, fig. 3), we interpret this process as directing the action of the stapedius muscle, which runs in the narrow gap between the crista interfenestralis and the medial wall of the facial sulcus (see below).

Posterior and lateral to the promontorium are the visible surfaces of the pars canalicularis (Fig. 4C), which contribute to the roof of the tympanic cavity proper. The posterior part is broader than the lateral and is divided into two subequal spaces by a slight ridge that extends posteriorly from the lateral aspect of the cochlear fossula. The medial space, behind the cochlear fossula, is a slight depression, wider than long, the post-promontorial tympanic sinus (Fig. 4C), which lodges a diverticulum of the cavum tympani in life. The lateral space is longer than wide and is bounded laterally by the facial canal (described separately below). In the posterolateral aspect of the lateral space is the nearly circular fossa for the stapedius muscle (the anterior part of which is visible in Fig. 4C). The posterior wall of the post-promontorial tympanic sinus and the stapedius fossa is formed by the posterior bullar wall, the dorsal base of which includes a narrow contribution from the pars canalicularis. This low ridge on the pars canalicularis represents the medial section of the caudal tympanic process of the petrosal (sensu MacPhee 1981). The border between the caudal tympanic process and the remaining posterior bullar wall is indicated by the passage of a nerve, the auricular ramus of the vagus nerve, remnants of which are preserved in FMNH 28350. In the sectioned fetus, the auricular ramus runs across the posteroventral surface of the cartilaginous pars canalicularis (visible in the fetus in Fig. 17) and connects the vagus nerve below the jugular foramen with the facial nerve at the stylomastoid foramen. In FMNH 28350, a small aperture between the pars canalicularis and the remaining bullar wall below the posterolateral corner of

the jugular foramen leads into a canal for the auricular ramus of the vagus, filled with dried nervous tissue, between the same two osseous elements. This canal runs behind the post-promontorial tympanic sinus and the stapedius fossa and joins the facial canal proximal to the stylomastoid foramen.

The stapedius fossa in the sectioned fetus is unusual in that there are two separate muscles attached there (Fig. 17), each innervated by the same branch of the facial nerve. The principal occupant is the stapedius muscle, which attaches to the stapes. Posterolateral to the stapedius muscle is a much smaller muscle that attaches from the stapedius fossa to the stylohyal. In these attachments, this muscle resembles the levator hyoidei of monotremes (Edgeworth 1931, 1935). The levator hyoidei is considered to be the phylogenetic precursor of the stapedius muscle, because for example in *Dasyurus* the ontogenetic early attachment of the stapedius muscle is to the stylohyal and then secondarily to the stapes (Edgeworth 1914, 1935). The meaning or identity of the small levator hyoidei-like muscle of the fetal yellow armadillo is uncertain and requires additional study. Such a muscle has not been reported in other armadillo prenatal stages (*Dasyurus*, Edgeworth 1923; Reinbach 1952a, 1952b; Werner 1960; *Zaedyus*, Reinbach 1955) or adult armadillos (*Euphractus*, Ardouin 1937; *Dasyurus*, Kawano 1924).

The part of the pars canicularis lateral to the promontorium is a narrow shelf with one major feature, a longitudinal sulcus for the facial nerve and its greater petrosal branch (Fig. 4C). Although this sulcus is one continuous structure extending from the lateral edge of the epitympanic wing to behind the promontorium, it is best described as three separate entities named for the differing nervous contents: the cavum supracochleare, the facial sulcus, and the sulcus for the greater petrosal nerve. The structure delimiting the three entities is the primary facial foramen, which sits anterior to the fenestra vestibuli (hidden from view in the medial wall of the sulcus in Fig. 4). Based on the fetus, the primary facial foramen transmits the facial nerve from the internal acoustic meatus on the endocranial surface. Upon entering the sulcus, the facial nerve has an enlargement, the geniculate ganglion, and so the space occupied by the ganglion lateral to the primary facial foramen within the sulcus is the cavum supracochleare (sensu Gaupp 1908) (Fig. 4C). The facial nerve runs posteriorly from the geniculate ganglion within the facial sulcus. The greater petrosal nerve, a branch of the facial nerve, runs forward from the geniculate ganglion within what we call here the sulcus for the greater petrosal nerve (undercover of the "processus cristae facialis" in Fig. 4C). What is unusual about the cavum supracochleare and these sulci in the yellow armadillo is their continuity; usually in therians, the cavum supracochleare is floored by bone, which produces a secondary facial foramen transmitting the facial nerve posteriorly

into the facial sulcus and a hiatus Fallopii transmitting the greater petrosal nerve anteriorly (Wible 1990, 2003).

The cavum supracochleare (Fig. 4C) is wider than the facial sulcus behind it and with a much more prominent lateral wall. That wall abuts and is hidden by a triangular shelf ("processus cristae facialis" in Fig. 4C) that is continuous with the anterior wall of the auditory bulla and is thicker ventrally at that contact; the lateral edge of this triangular shelf forms the anteroventral margin of the large aperture connecting the tympanic cavity proper and the epitympanic sinus. The composition of the triangular shelf is uncertain in FMNH 28350; sutures delimiting the petrosal, entotympanic, and ectotympanic are not visible. Patterson et al. (1989: 21) described this structure in euphractines, but it is unclear whether these authors believed the triangular shelf to be petrosal or entotympanic in origin. The lateral wall of the yellow armadillo cavum supracochleare corresponds to the cartilaginous tegmen tympani of the auditory capsule of the prenatal *Dasyurus* and *Zaedyus* described by Reinbach (1955a, 1952b, 1955). In these forms and in the fetal yellow armadillo (Fig. 16), the tegmen tympani is unusual in that it is oblique, rather than merely horizontal, to the cochlear housing. It extends into the tympanic cavity proper rather than merely forming the roof, and its anteroventral end is club-shaped. In non-euphractine armadillos, the anteroventral end of the ossified tegmen tympani is expanded into an irregular, anteromedioventrally directed, often cup-shaped process that may (e.g., *Dasyurus novemcinctus* CM 97444) or may not (e.g., *Dasyurus kappleri* CM 76828) contact the anterior crus of the ectotympanic. Patterson et al. (1989) coined the term processus cristae facialis for this structure, noting its continuity posteriorly with the crista facialis (=crista parotica). In the yellow armadillo, it is unclear whether the triangular shelf that is continuous anteriorly with the auditory bulla is the processus cristae facialis (and secondarily fused to the anterior bullar wall) or is a bullar shelf (largely of entotympanic origin) underlying (and fused to) the processus cristae facialis. Until we have the opportunity to study juveniles retaining sutures in this region, we identify the triangular shelf in yellow armadillos as the "processus cristae facialis," using quotes because this structure resembles the processus cristae facialis of non-euphractines, but may not be derived from the same element, i.e., the tegmen tympani.

The sulcus for the greater petrosal nerve is not visible in Figure 4 as it is hidden by the "processus cristae facialis." It is occupied by the dried nerve in FMNH 28350, parallels the lateral edge of the epitympanic wing, and anteriorly disappears under cover of the auditory bulla. The sulcus is defined by a low medial wall, the lateral margin of the epitympanic wing; laterally, it grades into a hidden, flat area. Based on the fetus, we interpret the greater petrosal nerve as exiting the middle ear beneath the piriform fenestra and joining the deep petrosal

al nerve beneath the carotid foramen to form the nerve of the pterygoid canal.

Facial nerve structures are not the only occupants of the narrow interval between the tegmen tympani, the promontorium, and the epitympanic wing. Based on the fetus, the tensor tympani muscle attaches to the ventromedial side of the tegmen tympani (Fig. 16), and thus would have been hidden from view by the "proeessus cristae facialis." In addition, in the fetus there are some tiny arteries and nerves in the vicinity. At the anterior aspect of the middle ear, lateral to the greater petrosal nerve, are a rostral tympanic artery, off the maxillary artery, and a lesser petrosal nerve en route to the otic ganglion, on the mandibular nerve posteroventral to the foramen ovale. These structures run posteriorly dorsolateral to the anteroventral end of the tegmen tympani. They pass through the tegmen tympani (the artery is labeled the ramus inferior in Fig. 16) and continue posteriorly between the tensor tympani muscle and tegmen tympani. The nerve could not be traced further posteriorly. Posterior to the primary facial foramen, the artery bifurcates into a short branch continuing posteriorly lateral to the facial nerve and a long branch that runs dorsally through the posterior tegmen tympani to join the large arteria diploëtica magna (see below). We could not determine whether an aperture through the tegmen tympani for these structures exists in FMNH 28350, because the relevant area is hidden by the "processus cristae facialis." In their courses, these arteries appear to be remnants of the stapedia artery system (Wible 1984, 1987); only study of early ontogenetic stages can confirm that. The rostral tympanic artery is equivalent to the ramus inferior of the stapedia; the artery connecting to the arteria diploëtica magna through the tympanic roof is the ramus superior of the stapedia; and the artery running posterior with the facial nerve is the stapedia artery itself. The main stem of the stapedia artery off the internal carotid is absent in the injected adult *Euphractus sexcinctus* (= *Dasyurus setosus*) described by Tandler (1901). None of the small intratympanic arteries that we found in the sectioned fetus was reported by Tandler (1901). However, his report considers the major arteries only, and so his omission may not reflect the adult condition.

The subsequent course of the facial nerve posterior to the cavum supracochleare can be divided into three subequal segments: an open anterior segment in the facial sulcus, an enclosed middle segment in the facial canal, and an open posterior segment on the anterior surface of the mastoid process of Patterson et al. (1989), which we term the paroccipital process here. The open anterior segment is essentially opposite the fenestra vestibuli (facial sulcus in Fig. 4C). Its medial and lateral walls are low, except posteriorly where the medial wall has a distinct triangular process, medial to which runs the stapedius muscle. The lateral wall forms the dorsal margin of the aperture connecting the tympanic cavity proper and the epitympanic sinus.

In the enclosed middle segment (facial canal in Fig. 4C), the posterior continuation of the lateral wall of the facial sulcus can be described as having a lambdoidal bifurcation into medial and lateral arms, both of which curve posterodorsally and abut the posteromedial roof of the external acoustic meatus. The more anteroventrally projecting lateral arm borders the aperture connecting the tympanic cavity proper and the epitympanic sinus; the medial arm is the crista parotica (Fig. 4C). Between these two arms is a small ovoid depression, the fossa incudis (Fig. 4C), for the crus breve of the incus (Fig. 6). A bony depression housing the epitympanic recess, the space over the mallear-incudal articulation, is lacking; this ossicular articulation overlies the facial sulcus. The facial canal runs within the crista parotica (Fig. 4C). Neither its anterior nor posterior openings are visible in direct or oblique ventral views; the former is under cover of the anterior part of the crista parotica, the latter is in the posteromedial corner of the external acoustic meatus roof, hidden by the paroccipital process. (As noted by Patterson et al. 1989, the posterior opening is the equivalent of the stylomastoid foramen of *Dasyurus*.) The facial canal can be traced between these anterior and posterior openings, because the preserved dried nervous tissue within it is visible through the thin bony wall. The exact identity of the contributing bony elements to the facial canal is not clear. The anterior opening is clearly within the petrosal; the posterior opening is clearly between the petrosal (paroccipital process) and the ectotympanic. Although sutures indicating the change in composition are not preserved, we think it occurred at the ventral surface of the external acoustic meatus roof. It is also uncertain what relationship if any the tympanohyal, the proximal part of Reichert's (hyoid) cartilage, has to the facial canal. Patterson et al. (1989) noted it in young individuals medial to the ectotympanic and contributing to the facial canal, but they did not provide details of its contribution.

The open posterior segment of the facial nerve course is along the anterior surface of the paroccipital process (not visible in the figures). The nerve here is in fact within the external acoustic meatus, as occurs in other euphractines but which is very unusual in plaeentals (Patterson et al. 1989). The nerve leaves the external acoustic meatus in FMNH 28350 via a large, irregular aperture in the posterior wall of the meatus, between the paroccipital process and the ectotympanic. Guth (1961) called this aperture the foramen stylo-mastoïdien secondaire and the posterior opening of the facial canal, the foramen stylo-mastoïdien primitif. However, Patterson et al. (1989) correctly observed that the posterior opening of the facial canal is the foramen stylomastoïdeum definitivum, the foramen stylomastoïdeum primitivum being the place proximal to this where the nerve crosses the tympanohyal (see MacPhee 1981). Patterson et al. (1989) termed the irregular opening in the euphractine external

acoustic meatus a foramen stylomastoideum tertium, which we follow here (Figs. 2B, 4A, B). In CM 10743, the floor of the external acoustic meatus is not yet fully closed by the ectotympanic, and the foramen stylomastoideum is confluent with the external opening or porus of the external acoustic meatus (Fig. 9D). In the sectioned fetus, a small stylomastoid artery off the occipital artery accompanies the facial nerve into the middle ear via the foramen stylomastoideum primitivum (the definitivum and tertium are yet to form).

The petrosal contributes to the borders of four extratympanic foramina that are partially or fully hidden in ventral view by the auditory bulla. Anteromedially are the carotid foramen (Fig. 4) and narrow piriform fenestra, already described with the basisphenoid. Posteromedially are the jugular foramen and the foramen for the inferior petrosal sinus (Fig. 4). The jugular foramen lies medial to the post-promontorial tympanic sinus, separated from that space by the auditory bulla. It has the shape of a ship's hull in lateral view; the keel is formed by the exoccipital (based on CM 10743, which preserves a suture between the exoccipital and basioccipital), the deck by the petrosal. Deep within the jugular foramen, the petrosal bulges into the opening and nearly divides the space into anteromedial and posterolateral passageways. In the sectioned fetus, exiting the anterior part of the jugular foramen are the glossopharyngeal, vagus, and accessory nerves, and the sigmoid sinus and a caudal meningeal branch of the occipital artery occupy the posterior part. In some armadillos (e.g., *Dasypus kappleri* CM 76828), the cochlear canaliculus for the perilymphatic duct is visible in the jugular foramen's lateral wall. This is not the case in the yellow armadillo; the cochlear canaliculus is entirely within the cranial cavity and in fact can be seen there by looking through the foramen magnum. The sectioned fetus exhibits the adult pattern, with a cochlear canaliculus for the perilymphatic duct and accompanying vein within the cranial cavity (Fig. 17). Anterior to the jugular foramen is a small, separate, horizontal opening, which based on the fetus transmits the inferior petrosal sinus; Patterson et al. (1989: 22) incorrectly identified this aperture as transmitting an unnamed artery. This vein runs posteriorly from the cavernous sinus around the hypophysis and unites with the sigmoid sinus below the jugular foramen to form the internal jugular vein. Four bones contribute to the foramen for the inferior petrosal sinus, based on CM 10743: the petrosal dorsolaterally, the entotympanic ventrolaterally, the exoccipital dorsomedially, and the basioccipital ventromedially. Given that a sulcus for the inferior petrosal sinus cannot be seen endocranially through the foramen magnum, at least the posterior part of the course for the inferior petrosal sinus must have been within a canal between the petrosal and basioccipital.

Also visible in ventral view, behind the ectotympanic is the posterior surface of the paroccipital process

(Figs. 2B, 4); it will be described more fully with the mastoid or occipital view below.

Mastoid View (Fig. 5).—The mastoid exposure of the pars canicularis of the petrosal forms the ventrolateral surface of the occiput; it is taller than it is wide. Sutures clearly delimit the petrosal from its neighbors in FMNH 28350 except along its ventromedial margin where it is fused with the auditory bulla. Medially, the petrosal contacts the occipital surface of the exoccipital at a straight suture that runs slightly medially from ventral to dorsal. Dorsolateral to that, the petrosal has a short, curved suture with the supraoccipital, which is the concave member of the curve. Lateral to that is a broad, sinuous suture with the squamosal that extends onto the dorsolateral margin of the petrosal. Ventral to that, the petrosal abuts the posterolateral margin of the osseous external acoustic meatus. The lateral part of the ventral margin of the petrosal is the freestanding paroccipital process, and medial to that, the petrosal is fused with the auditory bulla.

In the middle of ventromedial margin of the petrosal is a round structure that sits within a shallow, round depression (stylohyal fossa in Fig. 5B). According to previous workers (e.g., Kampen 1905; Patterson et al. 1989), this depression is for the reception of the stylohyal element of the hyoid arch and is termed the stylohyal fossa by Patterson et al. (1992); the round structure within the fossa is the terminal end of the tympanohyal. Between this depression and the exoccipital in FMNH 28350 is what we interpret as a remnant of the suture between the petrosal and the auditory bulla; there is no indication of this suture lateral to the stylohyal fossa. Confirming our identification of a suture is CM 10743, which clearly shows that the stylohyal fossa lies in the suture between the petrosal and the auditory bulla. The portion of the petrosal immediately dorsal to the stylohyal fossa is the caudal tympanic process of the petrosal described above.

The ventrolateral margin of the petrosal is formed by a U-shaped paroccipital process (Fig. 5) that does not lie in the same plane as the remainder of the mastoid exposure; it is slanted forward, and its anterior surface is turned medially and its posterior surface is visible in lateral view (Fig. 2C). The bottom of the U forms the posterior border of the foramen stylomastoideum tertium (Figs. 2C, 4); the medial and lateral arms of the U contact the ectotympanic, the posterior crus and anterior crus, respectively. In FMNH 28350 (Fig. 5), the exterior surface of the U is smooth, which is in contrast to the rough exterior surface of the mastoid exposure dorsal to the U; this distinction is not present in the remaining specimens studied by us, in which both surfaces are smooth, except for CM 6399 in which the right side is rough. In all specimens, there is a distinct rounded prominence where the U and the mastoid exposure above it meet. The position of this varies in that it is closer to the medial arm of the U

in FMNH 28350 (Fig. 5) and CM 101007, closer to the lateral arm of the *U* in CM 6399, 61426, and 10743, and centrally located in CM 6398.

In the sectioned fetus, attaching to the ventral margin of the *U* are two muscles, both of which also attach to the stylohyal (Reichert's cartilage): ventrally is the well-developed posterior digastric and dorsally is the small mastoideostyloideus (Fig. 17). Not reported previously in armadillos, the latter is widely distributed among placentals and sometimes is fused to the posterior digastric (Saban 1968). Regarding the former, conflicting reports on the armadillo digastric exist in the literature. For example, it is reported to be absent in *Dasypus novemcinctus* (= *Tatusia novemcincta*, Bijvoet 1908) and *ChaetophRACTUS villosus* (= *Dasypus villosus*, Windle and Parsons 1899), monogastric in *Euphractus sexcinctus* (= *Dasypus sexcinctus*, Macalister 1869, 1873), and small with two heads in *Chlamyphorus truncatus* (= *Chlamyphorus truncatus*, Macalister 1873). The sectioned yellow armadillo fetus studied by us clearly has a two-bellied digastric muscle separated by a long tendon. The remaining surface of the *U* and most of the mastoid exposure immediately dorsal to it are covered by the well-developed sternomastoid muscle (Fig. 17). Posteromedial to this attachment, dorsal to the *U*, is an epaxial muscle that resembles the splenius capitis described for *Chlamyphorus* (= *Chlamyphorus*) by Macalister (1873) and *Dasypus septemcinctus* by Guth (1961).

The *U*-shaped paroccipital process is identified as the mastoid process by previous researchers (e.g., Guth 1961; Patterson et al. 1989). In his monographic treatment of the development of the ear region in various placentals, MacPhee (1981: 57) explicitly avoided the term mastoid process because "it is used in a great variety of senses." We concur with MacPhee's assessment. For example, mastoid process is included in the *Nomina Anatomica Veterinaria* (1994), but its usage in the anatomical literature of domesticated animals (e.g., Sisson 1910; Evans 1993) is equivalent to the mastoid exposure, that is, the part of the petrosal exposed on the occiput. MacPhee (1981: 57) employed the neutral term mastoid eminence for "an enlargement of the lateral part of the mastoid region." However, we suggest that a more appropriate term, paroccipital process, already exists and correctly reflects homology. The term paroccipital process is deeply embedded in the literature on non-mammalian cynodonts and Mesozoic mammals where it is used for a process on the petrosal (or opisthotic and prootic) that is divided into anterior and posterior parts for attachment of the quadrate/ineus and muscle, respectively (Crompton 1958; Luo 1994). In more derived forms (e.g., the Early Cretaceous prototribosphenidan *Vincelestes*, Rougier et al. 1992; Rougier 1993), the anterior part of the paroccipital process is the crista parotica, to which the tympanohyal is attached, and the posterior

part is a museular process termed simply the paroccipital process. *Dasypus kappleri* CM 76828 has a rounded prominence posterolateral to the stylomastoid foramen that resembles the paroccipital process of *Vincelestes*, except that it is slightly more laterally positioned. In light of this resemblance, we employ the term paroccipital process for the prominence in *D. kappleri*. The *U*-shaped paroccipital process in the yellow armadillo resembles that of *D. kappleri*, except that it is slightly more laterally positioned and rather than rounded it is anteroposteriorly compressed. A potential source of confusion with the term paroccipital process is that some authors (e.g., Gregory 1910) have applied it to the large muscular process of the exoccipital bone. However, the base and tip of that process are, respectively, the jugular process and paracondylar process of the *Nomina Anatomica Veterinaria* (1994); the latter is sometimes referred to as the paramastoid process (Sisson 1910; Greene 1935). Interestingly, the muscle that attaches to the tip of the *U* in the fetal yellow armadillo, the posterior digastric, attaches to the jugular process of the exoccipital of the dog (Evans 1993). The jugular process is lacking in *Vincelestes* (Rougier et al. 1992; Rougier 1993) and basal metatherians (Marshall and Muizon 1995; Muizon 1998) and eutherians (Kielan-Jaworowska 1981; Wible et al. 2004), and therefore the absence of this process in most of our yellow armadillo specimens (see exoccipital below) and many other dasypodids is likely a retained primitive state. Apparently, the jugular process to which the posterior digastric muscle is attached in various marsupials (e.g., *Didelphis*, Turnbull 1970) and placentals (e.g., *Canis*, Evans 1993) has evolved independently, capturing the musculature attached to the paroccipital process primitively.

The mastoid surface dorsomedial to the paroccipital process is dominated by a well-developed, deep, near vertical vascular sulcus (occipital groove in Fig. 5B). This sulcus does not extend all the way to the ventromedial border of the mastoid surface, but is separated from the stylohyal fossa by a gap. On the right side of CM 6399 and 101007, near the midpoint of the occipital groove is a narrow bridge of bone that encircles the groove. On both sides of CM 6398, this bridge is present, but incomplete; it extends from the medial wall of the groove but is separated from the lateral wall by a narrow gap. Dorsally near the supraoccipital border, the sulcus leads to two subequal, circular, anterodorsally directed foramina, one situated superior to the other (Fig. 5). In FMNH 28350, both foramina are completely within the petrosal, but the slightly smaller superior foramen in the remaining specimens has a small contribution from the supraoccipital. In addition to the two large foramina, there are seven or so tiny foramina asymmetrically arranged within the surface of the sulcus in FMNH 28350; fewer in the remaining specimens. Previous authors (e.g., Guth 1961; Patterson et al. 1989) identified

the larger ventral foramen and sulcus as for the mastoid vein. However, based on the sectioned fetus and an adult of *Euphractus sexcinctus* (= *Dasyurus setosus*) reported by Tandler (1901) and on adults of other armadillos (Hyrtl 1854; Tandler 1899; Bugge 1979), the main occupant of the larger ventral foramen is arterial, the arteria diploëtica magna (sensu Hyrtl 1853, 1854), the largest branch of the occipital artery. Based on the sectioned fetus, we think that the smaller dorsal foramen transmits an accompanying vein, the vena diploëtica magna. The sulcus contains both an artery and vein, which we identify as the occipital artery and vein based on CM 6398, 6399, 61426, and 101007 where the occipital groove for the occipital vessels continues dorsally onto the supraoccipital bone. In those mammals (e.g., monotremes) that have an arteria and vena diploëtica magna, these vessels typically enter the skull together via one aperture, the posterior opening of the posttemporal canal, and travel forward within the posttemporal canal, between the squamosal and petrosal (Wible and Hopson 1995). The fetal yellow armadillo conforms to this pattern, but the artery and vein occupy the extreme ventral and dorsal apices of the posttemporal canal, fully separated from each other. We think that this separation is retained in the adult with the formation of a bony partition subdividing the posterior opening of the posttemporal canal into ventral and dorsal foramina. Based on what is visible from the occiput, it appears that the posttemporal canal is also similarly subdivided, that is the dorsal and ventral foramina lead into separate canals. We cannot determine the rostral extent of that separation.

Auditory Bulla

The basicranium of FMNH 28350 is dominated by paired dome-shaped structures from which elongate tubes project laterally (Figs. 1B, 2B, 9). We identify the dome as the auditory bulla and the tube as the cylindrical external acoustic meatus. The cylindrical external acoustic meatus floors the outer ear canal, the lateral opening of which is the external acoustic porus (Fig. 3A). Most of the auditory bulla floors the middle ear and so represents the tympanic floor. The position of the tympanum, which separates the outer and middle ear, is marked in mammals by the sulcus tympanicus and dorsal to it, the crista tympanica (MacPhee 1981). In FMNH 28350, a horizontal cut through the right auditory bulla and the medial part of the external acoustic meatus was made prior to the publication by Patterson et al. (1989), exposing the position of the sulcus tympanicus and the crista tympanica (Fig. 4C). These structures are obliquely positioned and recessed slightly medially from the head of the cylindrical external acoustic meatus. Consequently, the lateralmost part of the dome actually floors the proximal external acoustic meatus and not the middle ear; therefore, the lateral part of the dome is not the tympanic floor per se. As a descriptive

term for the part of the outer ear medial to the cylindrical part of the external acoustic meatus, within the auditory bulla, Klaauw (1931) employed the term recessus meatus acustici externi, shortened to recessus meatus by McDowell (1958). In light of this, the medial two-thirds of the auditory bulla in FMNH 28350 is the tympanic floor and the lateral one-third is the recessus meatus.

There are no sutures indicating the presence of more than one contributing element to the auditory bulla and the cylindrical external acoustic meatus in FMNH 28350 (Figs. 1B, 2B) and in CM 6398, 6399, 61426, and 101007. In CM 10743, however, remnants of a roughly C-shaped oblique suture, with the opening between the arms of the C situated dorsolaterally, divide the auditory bulla into a medial one-third and a lateral two-thirds. In addition to sutural remnants, two elements are further demarcated by their external structure; the surface of the lateral element is smooth, whereas that of the medial contains minute foramina and grooves. Klaauw (1931: 274) reported that "the development of the auditory region of *Dasyurus sexcinctus* [= *Euphractus sexcinctus*] shows a well-developed cartilaginous entotympanic." In the sectioned yellow armadillo fetus studied here, only a ring-shaped ectotympanic bone contributes to the auditory bulla (Fig. 17); this specimen predates the formation of a separate entotympanic element. Following Klaauw (1931), we identify the medial and lateral parts of the bulla of CM 10743 as the entotympanic and the ectotympanic, respectively (labeled on FMNH 28350 in Fig. 2B); the cylindrical external acoustic meatus is formed by the ectotympanic, petrosal, and squamosal. Because CM 10743 is the only skull studied that indicates the composite nature of the bulla, it is the basis for the following descriptions of the external surfaces of the entotympanic and ectotympanic. Information on the intratympanic surfaces of these elements is based solely on the right side of FMNH 28350 (Fig. 4).

Entotympanic

Entotympanics are a category of independent cartilages that develop in the auditory bulla of various placentals and in most instances are ossified in the adult (Klaauw 1922; Novacek 1977; MacPhee 1979). Following Klaauw (1922), entotympanics are divided into two types, rostral and caudal, based on their approximate site of ontogenetic formation. Both rostral and caudal entotympanics have been reported in prenatal armadillos (*Dasyurus novemcinctus*, Klaauw 1922; Reinbach 1952b; *Zaedyus pichiy*, Reinbach 1955); the latter is the larger element contributing to the medial and posterior bullar walls, whereas the former is possibly an expanded cartilage of the auditory tube. We describe the entotympanic in CM 10743 as a single entity, because we do not know if two entotympanics are present or how they might be arranged.

The entotympanic in CM 10743 is roughly C-shaped, is underlain by the ectotympanic, and lies in the anterior, medial, and posterior walls of the auditory bulla (labeled on FMNH 28350 in Fig. 4C). Its external surfaces are essentially convex and, based on the right side of FMNH 28350, its intratympanic surfaces are essentially concave. The entotympanic's contribution to the external medial wall is the most substantial; the anterior and posterior arms taper from this thicker central part. Anteriorly, from medial to lateral, the entotympanic contacts the posterior face of the tympanic process of the pterygoid, of the tympanic process of the alisphenoid, and of the medialmost, weakest part of the entoglenoid process of the squamosal. Its only contact medially is with the petrosal, except in the vicinity of the foramen for the inferior petrosal sinus where it has a narrow contact with the basioccipital. In the anterior part of the medial wall, the entotympanic underlies the epitympanic wing of the petrosal; in the posterior part of the medial wall it underlies the medial edge of the pars canalicularis. Posteriorly, from medial to lateral, it contacts the exoccipital just lateral to the jugular foramen and the caudal tympanic process of the petrosal. The entotympanic forms the medial margin of the stylohyal fossa; the ventral margin is formed by the ectotympanic, and the remaining borders by the petrosal. In contrast to CM 10743, the contact with the basioccipital in FMNH 28350 (Figs. 4A, B) and in CM 6398, 6399, 61246, and 101077 is very broad, extending between the foramen for the inferior petrosal sinus and the basisphenoid-basioccipital suture (in the case of the CM specimens the entotympanic extends beyond the suture to the earotid foramen). This broad contact obscures the contact between the entotympanic and the epitympanic wing of the petrosal in these specimens.

The entotympanic contributes to the passageways for various soft-tissue structures. The auditory tube (Eustachian tube) enters the middle ear via a small, round, medially directed opening in the anteromedial suture between the entotympanic and the ectotympanic in CM 10743, the musculotubal canal (labeled on FMNH 28350 in Fig. 2B). The internal carotid artery and accompanying nerve run in a deep, longitudinal sulcus in the part of the entotympanic underlying the epitympanic wing of the petrosal (Fig. 4C). This earotid sulcus leads to the carotid foramen, which is principally between the basisphenoid and petrosal, but which is floored posteriorly by the entotympanic (Fig. 4C). This sulcus is open bilaterally in FMNH 28350, CM 6398, 10743, and on the left side of CM 61426, but it is closed by a narrow bridge at its anterior end bilaterally in CM 6399 and 101007 and on the right side of CM 61426 (Fig. 9). At the posteromedial aspect of the auditory bulla are three foramina to which the entotympanic contributes (already described with the petrosal above); from anterior to posterior these are the foramen for the inferior petrosal sinus, the jugular

foramen, and the canal for the auricular ramus of the vagus (all but the last are visible in Fig. 4C).

FMNH 28350 provides some details about the intratympanic anatomy of the entotympanic. Posteriorly, in the contact between the entotympanic and the caudal tympanic process of the petrosal, is the canal for the auricular ramus of the vagus. Medially and anteriorly (Fig. 4C), the entotympanic has a broad contact with the overlying epitympanic wing of the petrosal; it is anteriorly that there are the two small venous foramina between the entotympanic and the epitympanic wing of the petrosal mentioned above. As discussed above (see petrosal), anterolaterally, the entotympanic may form the "processus cristae facialis" (Fig. 4C), the horizontal, triangular shelf that underlies the tegmen tympani, and may provide some attachment area for the tensor tympani muscle. The lateral wall of this shelf forms the anterodorsal margin of the opening between the tympanic cavity proper and the epitympanic sinus (Fig. 4C).

Ectotympanic

The intramembranous ectotympanic can be divided into two parts: a medial part contributing to the auditory bulla and a lateral part contributing to the cylindrical external acoustic meatus (Figs. 1B, 2B). In CM 10743, the transition between the two parts is marked by a change externally from a smooth surface medially to one riddled with tiny openings and grooves laterally; the remaining specimens show smooth external surfaces (Fig. 1B).

Like the entotympanic against which it abuts, the medial or bullar part of the intramembranous ectotympanic in CM 10743 is roughly C-shaped; the anterior and posterior arms of the C represent the anterior crus and posterior crus of the ectotympanic, respectively. The external surfaces of the C are convex and, based on the right side of FMNH 28350, the intratympanic surfaces are concave. It is on the internal surface of the C that the crista tympanica (Fig. 4C) and the sulcus tympanicus occur; the tympanum attaches to the sulcus tympanicus with the crista marking the dorsal edge of the sulcus. The sulcus tympanicus divides the medial part of the ectotympanic into two: the tympanic floor and the recessus meatus, medial and lateral to the sulcus tympanicus, respectively. Based on the right side of FMNH 28350, the contribution of the ectotympanic to the latter is considerably smaller than the former. In addition to the entotympanic, the external surface of the medial part of the ectotympanic contacts the entoglenoid process of the squamosal anteriorly and the stylohyal fossa and the paroccipital process posteriorly. In the contact between the squamosal and the ectotympanic, the curved, club-shaped, ventrally directed anterior process of the malleus is present on the right side of CM 10743, but absent from the remaining sample. Medial to the anterior process of the malleus is the Glaserian fissure (labeled on FMNH 28350 in Fig. 4C).

for the chorda tympani nerve. At the anteromedial corner of the ectotympanic is the small, round, medially directed opening for the auditory tube or musculotubal canal (Fig. 2B), which lies in the suture between the ectotympanic and entotympanic in CM 10743.

The lateral part of the ectotympanic is one of three elements contributing to the osseous, cylindrical external acoustic meatus, the others being the paroccipital process of the petrosal and the postglenoid region of the squamosal (Fig. 4C). The sutures between these three elements are blurred in FMNH 28350 and CM 6398, 6399, 61426, and 101007. However, CM 10743 has sutures delimiting the three. In addition, the bony floor of the external acoustic meatus is incomplete laterally in CM 10743 (Fig. 9D), in contrast to the more complete condition in the other specimens (Figs. 9A–C, E, F); this incomplete condition provides some developmental information on the attainment of the more complete state (see below). We describe the lateral part of the ectotympanic in CM 10743 in terms of its contribution to the four walls of the external acoustic meatus. The anterior, dorsal, and posterior walls are complete to the external acoustic porus; the ventral is not. The external surfaces of all walls are convex and the internal concave. There are two unequal elements in the anterior wall, the much larger anterior crus of the ectotympanic and the postglenoid process of the squamosal. The latter forms most of the anterior wall at the external acoustic porus (labeled on FMNH 28350 in Fig. 3A); the former forms the ventralmost part of the external acoustic porus and the bulk of the anterior wall medial to that. Sutures in the dorsal wall reveal the presence of three entities, a broad contribution from the squamosal laterally and equal, narrow contributions from the anterior crus of the ectotympanic anteromedially and the posterior crus posteromedially. The medial edges of the anterior and posterior crura are raised as the crista tympanica (labeled on FMNH 28350 in Fig. 4C). As a consequence of the contact between the anterior and posterior crura in the dorsal wall, the ectotympanic forms a complete ring about the tympanum. We cannot ascertain whether the suture between the two crura present in CM 10743 is retained in older specimens as this area is broken in FMNH 28350 (dashed line in Fig. 5C). The posterior wall also has three entities. Subequal in contribution are the paroccipital process, which forms the external acoustic porus and adjacent area, and the posterior crus of the ectotympanic, which lies anteromedial to the paroccipital process (labeled on FMNH 28350 in Figs. 4A, B). At the medial end of the posterior wall, the back surface of the posterior crus abuts the anterior surface of the paroccipital process, but lateral to that, the two elements are separated by a narrow gap. The third entity in the posterior wall is a small lip of squamosal on the anterodorsal face of the paroccipital process, which represents the posttympanic process (labeled on FMNH 28350 in Fig. 3A). As stated above, the ventral wall is incomplete in CM 10743

(Fig. 9D). It consists of a narrow shelf of bone projecting laterally from the recessus meatus part of the auditory bulla, roughly half the distance from the bulla to where the other walls contribute to the porus. The ventral wall is formed entirely by the ectotympanic.

The remaining specimens, FMNH 28350 (Figs. 2B, 4, 9A) and CM 6398, 6399, 61426, and 101007 (Figs. 9B, C, E, F), differ from CM 10743 in the fusion of sutures and in that the ventral wall extends laterally roughly to the same extent as the other three walls and contributes to the bony external acoustic porus. The ventral wall is not flat adjacent to the porus, but angled such that the porus is directed upward and outward (Fig. 5). Ossification of the ventral wall is not complete, and a sizeable ovoid gap remains in the middle of the ventral wall in front of the anteroventral tip of the paroccipital process (Fig. 2B). This gap is the foramen stylomastoideum tertium of Patterson et al. (1989). Based on CM 10743, it appears that the bulk of the ossification that forms the ventral wall adjacent to the porus in the other specimens is from the anterior crus of the ectotympanic (see also Patterson et al. 1989). The ventral wall adjacent to the porus presents differences among FMNH 28350 and CM 6398, 6399, 61426, and 101007. In FMNH 28350, the medial part of the ventral wall has a distinct ridge running parallel to the long axis of the meatus. Opposite the lateral aspect of the foramen stylomastoideum tertium, this ridge bifurcates into a low anterior arm and a more distinct posterior arm, which diverge laterally. In between these two ridges is a flat, but roughened, triangular surface. CM 6398, 6399, and 61426 resemble FMNH 28350 except that all the ridges are better developed and the triangular surface is smooth, not roughened. In addition, in CM 6399 the ridges converge again laterally, giving the enclosed area a teardrop shape. CM 101007, a female (the sex of the other specimens is unknown), resembles CM 6398 and 61426 except that midway along the anterior ridge of the triangular surface is a prominent process. The morphology of this region in these three specimens appears suited for muscle attachment, perhaps for the digastric on the neighboring paroccipital process.

Aspects of the internal anatomy of the ectotympanic have been discussed above (see petrosal). The absence of sutures between the ectotympanic and its neighbors in FMNH 28350, the only specimen with an open bulla, complicates our descriptions (Fig. 4). Despite this, it is clear that the ectotympanic contributes to two openings internally. It forms the entire ventrolateral border of the large opening connecting the middle ear proper and the epitympanic sinus (Fig. 4C). The parts of the ectotympanic forming this border are the anterior and posterior crura, at their contact in the roof of the external acoustic meatus. Posterolateral to this, in the roof of the external acoustic meatus, the posterior crus forms the anterior border of the stylomastoid foramen (not visible in the figures); the paroccipital process forms the posterior border.

Only one muscle arises from the ectotympanic in the sectioned yellow armadillo fetus. The levator veli palatini runs from the anteromedial corner of the ectotympanic to the soft palate in front of the auditory tube. In addition to its attachment to the pterygoid described above, the tensor veli palatini arises from dense connective fibers just anterior to the ectotympanic and anterodorsal to the origin of the levator veli palatini. In light of this position in the fetus, it seems likely that the tensor attaches to the ectotympanic and entotympanic in the adult. Kostanecki (1891: 162) reported the origin of the tensor veli palatini in *Dasypus sexcinctus* (= *Euphractus sexcinctus*) as the "Bulla tympanica" and the "Os sphenoides."

Middle-Ear Ossicles

The ear ossicles are not preserved on the right side of FMNH 28350 and could not be directly observed in the remaining specimens, including the left side of FMNH 28350, because they are hidden within the auditory bulla at the base of the long external auditory meatus. Therefore, we have based our description upon Guth's (1961) illustration of the auditory ossicles in *Euphractus sexcinctus*, redrawn here in Figure 6. As illustrated by Guth (1961: fig. 87), the ossicles are quite similar to those described and illustrated for *Euphractus* by Doran (1878) and Ardouin (1937), and for the closely related *ChaetophRACTUS villosus* (Patterson et al. 1992) and *Chlauphorus truncatus* (Fleischer 1973; Segall 1976). The description of the attachments between the ossicles and the surrounding auditory region elements are based upon direct observation of FMNH 28350, and, where possible, the remaining specimens.

Malleus

The malleus (Fig. 6) lies within the tympanic cavity. It is attached laterally to the tympanum. It forms a synovial articulation posteromedially with the incus, and its anterior process lies in a groove, the proximal portion of which traverses the ectotympanic. This groove emerges on the exterior surface of the skull just posterolateral to the Glaserian fissure, between the ectotympanic and the entoglenoid process of the squamosal (labeled on FMNH 28350 in Fig. 4C). The malleus is not attached to any other bony element in the skull.

The malleus of the yellow armadillo (Fig. 6) closely resembles that described for the closely related *ChaetophRACTUS* by Patterson et al. (1992). It is attached to the tympanum along the lateral surface of a ventrally directed process, the manubrium. At its base, the manubrium is anteroposteriorly compressed, but broad mediolaterally due to the presence of a distinct lateral process. The manubrium tapers distally in both its mediolateral and anteroposterior dimensions for approximate-

ly three-quarters of its total length, then expands again to form a spatulate, mediolaterally compressed tip. The manubrium is connected to the more dorsal portions of the bone by a short, mediolaterally compressed neck. In lateral view, the posterior edge of the neck is straight, the anterior edge concave. In contrast to the dog (Evans 1993), there is no indication of a muscular process in this region for the insertion of the tensor tympani muscle. Extending from the anterodorsal edge of the neck is the elongate anterior process of the malleus. In the juvenile yellow armadillo, CM 10743, the anterior tip of the anterior process is visible between the ectotympanic and the entoglenoid process of the squamosal on the right side only; it is expanded into a flat, club-shaped, anteroventrally directed process. The lamina, which lies at the proximal base of the anterior process immediately ventral to the head is similar in size to that found in *ChaetophRACTUS*. Patterson et al. (1992) observed that the lamina of *ChaetophRACTUS* is considerably smaller than that of *Dasypus*. The dorsalmost portion of the malleus is comprised of a swollen, almost globose, hemispherical head that extends dorsally into the epitympanic sinus. Posteriorly, the head carries two articular facets for the incus. The upper facet is vertical, faces posteriorly and slightly medially, and is considerably larger than the lower facet. The lower facet lies at slightly more than a 90-degree angle to the upper facet and is thus oriented just below the horizontal plane, facing dorsally and slightly posteriorly.

Incus

The incus (Fig. 6) also lies suspended within the tympanic cavity, posterior to the malleus and extending well into the epitympanic sinus. It forms a synovial articulation with the malleus anterolaterally, and is suspended from the skull by a ligament that connects its crus breve to the fossa incudis of the petrosal (the last is visible in FMNH 28350 in Fig. 4C). The incus has a rectangular body to which are attached two processes (Fig. 6). The body is compressed mediolaterally and bears two articular facets that match the corresponding facets on the malleus. The more dorsal facet is larger, and faces anteriorly and slightly laterally. The more ventral facet is oriented at a slightly obtuse angle to the former, and faces ventrally and somewhat laterally. The two processes attached to the body are the crus breve and crus longum. The crus breve extends almost directly posteriad from the body. It is short and triangular, tapering distally, and, as noted above, is connected by a ligament attached at its distal extremity to the fossa incudis of the petrosal. The crus longum is ventrally directed and is substantially longer than the crus breve. It has a triangular base that tapers distally, but re-expands at its distal extremity, where it bears an articular facet for the stapes. This articular facet is not visible laterally in the yellow armadillo (Fig. 6), but in the

dog (Evans 1993) and in specimens of the armadillo genus *Dasypus* (e.g., *D. novemcinctus* UTCM 15), which lacks an ossified auditory bulla, leaving the ossicles open to view, the stapedial facet is borne on a small but distinct process extending medially from the end of the crus longum, the mushroom-shaped os lenticulare.

Stapes

The stapes (Fig. 6) forms the third element in the ossicular chain that traverses the tympanic cavity. Unlike the other two ossicles, whose long axes lie in a vertical plane, the stapes is oriented horizontally. It is attached laterally to the os lenticulare of the incus, whereas medially, its oval base inserts into the fenestra vestibuli (the last is visible in FMNH 28350 in Fig. 4C), held in place there by an annular ligament. The stapes (Fig. 6) is comprised of a small head that attaches to the incus, two crura separated by a large, rounded, triangular intracranial foramen, and a base or footplate that sits in the fenestra vestibuli.

The stapedial head is short, and bears a relatively flat, oval, laterally directed facet at its tip (Fig. 6). Underneath its distal articular surface, the head is tapered toward its base, where it connects with the anterior and posterior crura. These are bowed somewhat anteriorly and posteriorly, particularly in their lateral portions, giving the stapes a "slightly convex" configuration according to the shape categories erected by Gaudin et al. (1996). There is no sign of a distinct muscular process on the posterior crus. Such a process is present in the dog (Evans 1993) and many other mammals at the insertion point of the stapedius muscle (Doran 1878; Fleischer 1973; Gaudin et al. 1996). The crura are thin and hollowed out medially, resulting in a semicircular cross section. They are connected at their bases by raised ridges that form the dorsomedial and ventromedial rims of the intracranial foramen, respectively. Although we do not have a specimen of the yellow armadillo in which the stapes can be observed *in situ*, in *Dasypus* (e.g., *D. novemcinctus* UTCM 15) the crura lie in roughly the same vertical plane, meaning that the anteroposterior axis of the stapes is roughly horizontal. The base or footplate of the stapes is oval, longer anteroposteriorly than dorsoventrally. As noted in the description of the petrosal, the stapedial ratio in *Euphractus* is approximately 1.9–2.0. The base extends as a thin rim around the proximal margins of the stapedial crura. It does not have a distinct medial convexity, as occurs in many other placental mammals (Doran 1878; Fleischer 1973; Gaudin et al. 1996).

Occipital Complex

The fetal yellow armadillo has four ossification centers in the occipital region of the chondrocranium: an anterior midline ossification, the basioccipital, in the central stem

opposite the rear of the pars cochlearis of the auditory capsule (visible in Fig. 17); a large posterior midline ossification, the supraoccipital, in the tectum synoticum, dorsal to the foramen magnum; and paired lateral ossifications, the exoccipitals, in the central stem between the jugular and hypoglossal foramina. CM 10742 is the only skull studied that preserved sutures between all four ossifications. In FMNH 28350 (Figs. 1B, 2B, 4A, B), the basioccipital and exoccipitals are fused seamlessly; sutures are preserved between the exoccipitals and supraoccipital (Fig. 5). In CM 6398, 6399, 10742, and 101007, all sutures are obliterated resulting in a single occipital bone, as occurs, for example, in the dog (Evans 1993); in fact, in these four yellow armadillo specimens, the occipital bone is fused to the sphenoid complex as well (Figs. 9B, C, E, F). The descriptions that follow of the individual bones of the occipital complex are based principally on FMNH 28350, with the placement of the basioccipital-exoccipital suture based on CM 10743.

Basioccipital

The unpaired basioccipital forms the flat skull base between the left and right ear regions (Figs. 1B, 2B) and is roughly hexagonal, based on CM 10743, the only specimen preserving the basioccipital-exoccipital suture (Fig. 9D).

The six sides of the basioccipital include unpaired anterior and posterior sides, and paired anterolateral and posterolateral sides. The anterior side, the suture with the basisphenoid (Fig. 2B), is the broadest; the remaining five sides are subequal in length. The basioccipital is at its broadest at the intersection of the anterolateral and posterolateral sides, and at its narrowest at its posterior side. Medially, the anterior side is straight, but laterally, it curves slightly posteriorly, just posterior to the carotid foramen. The paired anterolateral sides are straight, but angled slightly posterolaterally. Each is in contact with the entotympanic in FMNH 28350 (Figs. 2B, 4A, B) and CM 6398, 6399, 61426, and 101007. In contrast, in CM 10743 only the posteriormost anterolateral side abuts the entotympanic; the remaining surface contacts the petrosal. The paired posterolateral sides are the sutures with the exoccipitals, based on CM 10743. They are generally straight, but angled posteromedially. The unpaired posterior side is the odontoid notch for the dens of the axis (Figs. 4A, B).

At the intersection of the anteromedial and posterolateral sides of the basioccipital is the small, posteriorly directed foramen for the inferior petrosal sinus (Fig. 4). Based on CM 10743, this paired foramen lies between the basioccipital, exoccipital, petrosal, and entotympanic.

The ventral surface of the basioccipital is generally flat with three exceptions: paired muscular fossae and the odontoid notch (Figs. 4A, B). In the yellow armadillo fetus, two paired muscles attach to the basioccipital, adja-

cent to each other, medial to the pars cochlearis of the auditory capsule. Anteromedially is the larger longus capitis and posteromedially is the smaller rectus capitis ventralis (visible in the fetus in Fig. 17). FMNH 28350 (Figs. 4A, B) and CM 6398, 6399, 61426, and 101007 have a pair of well-developed fossae that probably house both muscles, but the morphology differs among these specimens; fossae have not yet formed in CM 10743 (Fig. 9). In FMNH 28350 (Figs. 4A, B) and CM 6399, the fossae are opposite the anterolateral side of the basioccipital, ovoid, and angled anteromedially; the posterior walls of the fossae are raised, producing a small tubercle. In CM 61426, the fossae are also ovoid, but smaller, without raised walls, and nearly horizontal. Finally, in CM 6398 and 101007, the fossae are larger, slightly more posteriorly positioned, teardrop-shaped with the tapered end pointing posteriorly, and with the anterior wall raised. The shape of the odontoid notch differs in the studied sample (Fig. 9). The odontoid notch has the shape of an inverted broad *U* in FMNH 28350 (Figs. 4A, B) and CM 10743 and 61426, with a narrow facet along the contour of the *U*, facing posteriorly, and with the edge (or lip) of the notch raised slightly. In contrast, in CM 101007, the odontoid notch is shallow and the facet extends anteriorly a short distance onto the ventral surface of the basioccipital, such that the bulk of the facet is directed ventrally or even anteroventrally. CM 6398 and 6399 also has a shallow odontoid notch, but with no facet at all.

Exoccipital

The paired exoccipitals have two roughly quadrangular parts: a horizontal one on the skull base (Figs. 2B, 4A, B) and a vertical one on the occiput (Fig. 5). Each part contributes to the lateral walls of the foramen magnum and the paired occipital condyles. Each part is described separately followed by a description of the condyle.

The horizontal part of the exoccipital (Figs. 4A, B) is roughly trapezoidal. The narrow side faces the foramen magnum; the broad side faces the ear region; the antero-medial side is the suture with the basioccipital; and the posterolateral side is the back of the occipital condyle. The anterolateral aspect of the horizontal part is dominated by a well-developed fossa within which the jugular foramen, the hypoglossal foramen, and the foramen for the inferior petrosal sinus open (Figs. 4A, B). (It is possible that the basioccipital may have a very small contribution to this fossa anteriorly, but we cannot confirm this because the fossa has not yet formed in CM 10743, the only specimen to preserve the basioccipital-exoccipital suture.) The exoccipital forms the medial border of the jugular foramen, described more fully above (see petrosal). Based on CM 10743, the exoccipital abuts the petrosal anteromedial to the jugular foramen, and the petrosal and the entotympanic posterolateral to that opening. The

anteroventrally directed hypoglossal foramen is entirely within the exoccipital, posteromedial to the jugular foramen. The number of hypoglossal foramina per side varies among the six specimens studied. One foramen is present bilaterally in CM 6398, 6399, and 101007, on the left side of FMNH 28350, and on the right side of CM 10743; two foramina are present bilaterally in CM 61426, on the right side of FMNH 28350 (Figs. 4A, B), and the left side of CM 10743. In addition, small foramina presumably nutritive in function are present in and around the hypoglossal foramina in all specimens; one of these is visible on the right side of FMNH 28350 in the ventral view (Figs. 4A, B). Posterolateral to the hypoglossal foramen, anterodorsal to the anterior edge of the occipital condyle are two or three small, presumably nutrient foramina, which we identify as ventral condyloid foramina in light of their occurrence in the ventral condyloid fossa (not visible in the figures). In the fetal yellow armadillo, only one hypoglossal foramen occurs per side; it transmits the hypoglossal nerve, a small caudal meningeal branch of the occipital artery, and a large vein that joins with the sigmoid and inferior petrosal sinuses below the skull to form the internal jugular vein. Bilaterally in FMNH 28350, there is a faint channel connecting the hypoglossal foramen and the foramen for the inferior petrosal sinus (Figs. 4A, B); this channel is more prominent bilaterally in CM 6398, 6399, and on the right side of CM 101007, but is not present on the latter specimen's left side or in CM 10743 and 61426 (Fig. 9). Based on the fetal yellow armadillo, this channel carries the inferior petrosal sinus into which the vein with the hypoglossal nerve flows; together these then join the sigmoid sinus to form the internal jugular vein.

The four sides of the vertical part of the exoccipital (Fig. 5) are ventrally the condyle; laterally the suture with the mastoid exposure of the petrosal, which is roughly straight but angled dorsomedially; dorsally the suture with the supraoccipital, which is also roughly straight but angled ventromedially; and medially the concave border of the foramen magnum. The bulk of the surface above the condyle is flat. In FMNH 28350, there is a shallow dorsal condyloid fossa into which two small foramina open; similarly situated nutrient foramina are present in the fetal yellow armadillo. The dorsal condyloid fossa is shallower in CM 101007 with three foramina on the right and two on the left; and much deeper in CM 6398 with two larger foramina on the left and one larger on the right and 61426 with one larger foramen bilaterally. CM 6399 also has a deep fossa, with one large and two small foramina on the left and two small foramina on the right. CM 10743 has a shallow fossa with some tiny foramina within, but it is hard to distinguish true foramina, because the immature bone is heavily pitted.

The occipital condyle is present on both the horizontal and vertical parts of the exoccipital (Figs. 2B, 4A, B, 5), although that on the horizontal part is somewhat

larger. The condyle is essentially cylindrical, with a convex medial border and a concave lateral border in FMNH 28350 and CM 6398, 6399, 10743, and 101007; the lateral border is convex in CM 61426. In CM 6398 and 6399, the concavity on the lateral border is U-shaped and bears a small pit. The anteroventral border forms the back of the fossa containing the jugular foramen, the hypoglossal foramen, and the foramen for the inferior petrosal sinus. The posterior border forms the ventral edge of the dorsal condyloid fossa.

In CM 6399, the area immediately lateral to the condyle at the junction of the horizontal and vertical parts of the exoccipital is raised into a rounded, rugose knob. This knob may represent a small jugular process like that described as the paroccipital process by Patterson et al. (1989) in *Priodontes*, *Cabassous*, *Proeutatus* (FMNH 13199), *Peltephilus*, pampatheres, and glyptodonts.

Supraoccipital

The unpaired supraoccipital forms the dorsal half of the occiput, the back of the nuchal crest, and the dorsal border of the foramen magnum (Fig. 5).

The supraoccipital (Fig. 5) is somewhat fan-shaped. The base of the fan completes the dorsal margin of the foramen magnum. The lateral margins of the fan are the sutures with the exoccipitals medially and the mastoid exposures of the petrosals laterally; the former is more or less straight and the latter is curved, with the supraoccipital the concave member. The bulk of the convex margin of the fan is the suture with the parietals, with a small contact with the squamosals ventrolaterally. The dorsal edge of the supraoccipital is thickened, more so laterally than medially, and forms the back of the nuchal crest; the front of the nuchal crest is formed principally by the parietals with a small contribution from the squamosals ventrolaterally. In dorsal view, the nuchal crest and the dorsal edge of the supraoccipital have the shape of a mustache. The supraoccipital immediately above the foramen magnum is relatively flat and devoid of features, although there is a narrow vertical groove of uncertain function on the midline that is present only in FMNH 28350. Dorsal to this is a raised vertical ridge, the external occipital crest, which reaches nearly to the nuchal crest (Fig. 5). On either side of the external occipital crest is a broad, shallow fossa that provides attachment for epaxial musculature. A variable number of small foramina are found in the supraoccipital. FMNH 28350 has two on the left side, one below the nuchal crest the other above the foramen magnum, and two on the right side above the mastoid exposure (Fig. 5). CM 6398 has three foramina per side below the nuchal crest and two per side lateral to the external occipital crest. CM 6399 has one foramen in the midline above the external occipital crest and below the nuchal crest, one foramen immediately to the left of the external occipital crest near the midpoint of the

crest, and perhaps two or three tiny foramina on either side just below the nuchal crest. CM 101007 has about a dozen per side just below the nuchal crest, and CM 61426 has about a dozen on the right and five on the left just below the nuchal crest. CM 10743 has no foramina in the supraoccipital.

Mandible

The paired mandibles consist of a narrow tooth-bearing horizontal part, or body, and a broad vertical part, or ramus (Figs. 1D, 7A). The left and right mandibles are united anteriorly at the mandibular symphysis, a rough-surfaced fibrous joint (Fig. 7B). Each mandible houses ten teeth, increasing in size through the first eight and decreasing thereafter (Fig. 7C). As with the upper teeth, the outer contour of the lower teeth also changes from more oval anteriorly to nearly circular posteriorly. In addition, the anterior teeth slant labially, whereas the posterior ones slant lingually. The sectioned fetus has nine pairs of tooth germs in the intramembranous mandibles: the first six and last are at a cap stage and the seventh and eighth at an early bell stage.

In lateral view (Figs. 7A, 10), the body of the mandible is elongate, deepest below the eighth tooth and tapering to a point anteriorly. The posterior half of the last tooth is hidden by the base of the coronoid process. The bulk of the lateral surface of the body is riddled with minute to tiny foramina and grooves, particularly in FMNH 28350 (Figs. 1D, 9A), suggesting the presence of a complex microvascular pattern. In FMNH 28350, four more substantial openings in the anterior mandible lead into anteriorly directed sulei and are identified as mental foramina (Fig. 7A) based on the fetus; three are on a horizontal line: the anteriormost below the front of the third tooth, the middle one below the back of the third tooth, and the posteriormost below the middle of the fifth tooth. Below the middle one is the fourth mental foramen. CM 10743, the left side of 6398 and 101007, and the right side of CM 6399 have only the three on a horizontal line, and CM 61425 (which preserves only the right mandible), the right side of 6398 and 101007, and the left side of CM 6399 have only two (Fig. 10). The sectioned fetus has three mental foramina that are continuous with the mandibular canal, which transmits the inferior alveolar nerve, artery, and vein. The anterior mental foramen transmits nerve, artery and vein, and lies below the gap between the second and third tooth germ; the posterior two foramina transmit only nerve and vein, and lie below the fifth tooth germ. The lateral surface in front of the first tooth is smooth, and based on the sectioned fetus and the study by Uekermann (1912) provides attachment for the mentalis muscle (Fig. 12). According to Uekermann (1912), the buccinator muscle arises from the outer part of the alveolar process and the rostral edge of the mandibular ramus. In the sectioned fetus, the buccinator

attaches to the lateral alveolar margin of the first six tooth germs; it approximates the anterior edge of the ramus, but has no attachment.

In medial view (Fig. 7B), the most conspicuous feature on the body of the mandible is the club-shaped rough surface of the mandibular symphysis, which extends from the rostral tip to below the front half of the fourth tooth. Posterior to that in FMNH 28350 are three faint narrow sulci with associated tiny foramina (Fig. 7B); the anterior two are longitudinal and the posterior one curves posterodorsally. For descriptive purposes, we designate these as the anterior, middle, and posterior mandibular sulci. The anterior sulcus lies roughly halfway between the dorsal and ventral margins of the mandibular body and extends from the posterior edge of the mandibular symphysis to below the front of the sixth tooth. It contains one tiny, slightly anteriorly directed foramen at its anterior end. The middle sulcus lies in a plane ventral to the anterior sulcus, extends from the gap between the fifth and sixth teeth to the middle of the eighth tooth, and contains three tiny, slightly anteriorly directed foramina and a fourth tiny, medially directed foramen. The posterior sulcus, the faintest of the three, appears to be in the same plane as the middle sulcus, extends from the back of the ninth tooth onto the mandibular ramus near the mandibular foramen, and contains one tiny, slightly posteriorly directed foramen at its anterior end. The occupants of these sulci are considered below. These sulci are wholly absent in CM 10743. In CM 61426, only the posterior sulcus is preserved, and in CM 6398 and 101007, there is a single longitudinal sulcus extending the same distance as the three in FMNH 28350. In CM 6399, the posterior, more dorsal longitudinal sulcus extends back from the level of the anterior portion of the fifth tooth on the right or the posterior portion of the sixth tooth on the left all the way back to a point directly beneath the mandibular foramen. On the left side, this groove is associated with two small anteriorly directed foramina at its anterior end. The anterior, more ventral sulcus extends from the middle of the fifth tooth to the posterior edge of the seventh tooth. It bears a small medially directed foramen on the left side only. The only other significant feature on the medial surface of the mandibular body is a low longitudinal ridge near the ventral border between the sixth and eighth teeth (see below). This ridge is more prominent in CM 6399, where it extends as a straight ridge from the posteroventral most point of the symphysis to the sixth tooth position, where it curves somewhat dorsally, ending at the level of the eighth tooth.

Four muscles attach to the ventromedial surface of the mandibular body in the sectioned fetus: the genioglossus, the geniohyoid, the mylohyoid, and the anterior digastric (all visible in the fetus in Fig. 13, except the geniohyoid). The genioglossus (with the geniohyoid behind it) is the most anterior and highest, attaching on a longitudinal line that begins behind the symphysis (below

the fourth tooth germ) and extends to the level of the seventh tooth germ; the geniohyoid arises from the back part of this line. The mylohyoid arises posteroventral to the genioglossus on a line that extends from below the fifth tooth germ nearly to below the mandibular foramen. This line is straight anteriorly but curves posterodorsally. The anterior digastric attaches posteroventral to the mylohyoid at the ventral margin of the body on a longitudinal line that extends from below the sixth tooth germ to behind the last tooth germ; in the posterior part of its mandibular attachment, the anterior digastric abuts the same muscle of the opposite side and grades into a tendon that connects across the midline (Fig. 15). We translate these attachments in the sectioned fetus onto the adult skull as follows (Fig. 7B). The genioglossus and the geniohyoid attach onto the smooth surface immediately below the anterior mandibular sulcus; the mylohyoid attaches onto the smooth surface immediately below the middle and posterior mandibular sulci; and the anterior digastric attaches onto the smooth surface below the low ridge. We found no evidence of a muscle attaching from the mandible to the sternum as has been reported for *Dasyurus novemcinctus* (= *Tatusia peba*, Macalister 1873; = *T. novemcincta*, Bijvoet 1908; Edgeworth 1923).

In occlusal view in FMNH 28350 (Fig. 7C) and CM 6399, the tip of the mandibular body in front of the first tooth has a small, ovoid opening, whose long axis is in line with the teeth behind it. This opening appears to be the remnant of a tooth alveolus. However, whether it was ever occupied is unknown. CM 6398 has a comparable opening on the right side, but on the left side are two smaller openings in its place. The other specimens do not have any such structure. There is also a small foramen posterolateral to the last tooth in FMNH 28350 (Fig. 7C) and CM 10743, but not in CM 6398, 6399, 61426, and 101007; the sectioned fetus has a corresponding foramen that is contiguous with the mandibular canal and transmits small branches of the inferior alveolar nerve, artery, and vein.

The ramus of the mandible has three salient processes, all lying dorsal to the alveolar plane: coronoid, condylar (articular), and angular (Figs. 7, 10). The coronoid process forms the anterodorsal part of the ramus and is somewhat shark fin-shaped, with the fin pointing posteriorly. Its base lies at near a right angle to the alveolar margin. Its anterior border, the coronoid crest, is thickened, especially dorsally, and strongly convex; its shorter posterior border is nearly straight. In CM 6398, 6399, 61426, and 101007, the anterior border of the coronoid process, from its dorsal tip to the level of the mandibular notch, is more than just thickened; it has a broad, raised surface (Fig. 10B, C, E, F). The condylar process is posteroventral to the coronoid, with a short neck at roughly 45 degrees to the alveolar margin. The ovoid articular surface faces dorsally, is transversely broad, and its axis lies at roughly a right angle to the alveolar plane. The central

part of the articular surface is slightly depressed compared to the medial and lateral lips, of which the former is slightly higher than the latter. The angular process lies posteroventral to the condyle, above the tooth row; it is also broadly shark fin-shaped, with the fin pointing dorsally. The ventral edge of the angle is thickened, strongly convex, and continuous with the thinner ventral margin of the ramus; the shorter dorsal border is concave and continuous with the back of the condylar process.

The lateral surface of the mandibular ramus is fairly smooth (Figs. 1D, 7A). There is a trace of an egg-shaped depression at the base of the coronoid process, above the level of the angular process. According to Smith and Redford (1990), no muscle attaches in this depression in the yellow armadillo; the masseter attaches to nearly the entire lateral surface ventral to this depression (Figs. 14, 15) and the temporalis is attached to the thickened anterior surface of the coronoid process. The most noteworthy feature on the medial surface of the ramus is the large, anteriorly directed mandibular foramen (Fig. 7B) for the inferior alveolar nerve and vessels. The foramen is situated roughly halfway between the last tooth and the angle, and its ventral edge lies at the alveolar plane. There is a large nearly circular depression immediately posterior to the foramen. A broad, straight, shallow sulcus for the mylohyoid nerve (see below) runs ventrally and slightly anteriorly from the depression behind the mandibular foramen nearly to the ventral margin of the ramus in FMNH 28350 (Fig. 7B) and CM 6398, 6399, 10743, and 101007; this sulcus is much narrower in CM 61426. Based on the sectioned fetus, the temporalis muscle has a broad attachment to the medial surface of the coronoid process (Fig. 15); the anteroventral limit of this attachment is indicated by an oblique line between the last tooth and mandibular foramen. The medial pterygoid muscle attaches to the medial surface of the angle and along the ventral margin of the ramus nearly to the level of the last tooth (Figs. 14, 15). The lateral pterygoid attaches to the medial surface of the condylar process above the neck. Lastly, attached to the posterior surface of the ramus immediately above the angle is one of the muscles of the external ear, the mandibulo-auricularis of Uekermann (1912).

Sulci are found on the medial side of the mandible in many Mesozoic mammals and extant therians, tending to be faint in the latter (Bensley 1902; Simpson 1928). In Mesozoic mammals, characters of these sulci frequently are used in phylogenetic analyses (e.g., Rougier et al. 1998; Ji et al. 2002). With few exceptions, the contents of these sulci in extinct and extant taxa are not known. Among extant mammals, there are few studies that provide details on the occupants of these sulci. Bensley (1902) examined pouch young of *Macropus* in order to infer the occupants of the mandibular sulci in extant adult mammals and in Mesozoic taxa. One of the recent forms figured and discussed by Bensley (1902, fig. 6) was the

long-nosed armadillo *Dasypus novemcinctus* (= *Tatusia novemcincta*), which showed two sulci: one resembling the mylohyoid sulcus of FMNH 28350 and the other the middle and posterior mandibular sulci of FMNH 28350 (Fig. 7B). Bensley (1902) identified the former as for the mylohyoid nerve and the latter as the Meckelian groove, an adult remnant of the deep groove that forms around Meckel's cartilage as the embryonic mandible develops.

Evidence provided by the sectioned fetus of *Euphractus sexcinctus* is relevant. The mylohyoid nerve and accompanying vein diverge from the inferior alveolar nerve behind the mandibular foramen and run anteroventrally along the mandibular ramus before turning forward ventral to the mylohyoid muscle (Fig. 14). There is little doubt that this nerve is the major occupant of the broad, shallow sulcus in the FMNH 28350 running ventrally and slightly anteriorly from the mandibular foramen to the ventral edge of the ramus. Consequently, Bensley (1902) correctly identified the similarly situated sulcus in *Dasypus novemcinctus*. However, the anatomy of the yellow armadillo fetus does not support Meckel's cartilage as the occupant of the longer, more longitudinal sulcus of *D. novemcinctus*. In the fetus, Meckel's cartilage does occupy a sulcus on the medial side of the mandible. From the mandibular foramen to below the gap between the eighth and ninth tooth germs, Meckel's cartilage lies ventral and parallel to the attachment of mylohyoid (Fig. 14), but anteriorly the cartilage is dorsal and parallel to that muscle (Fig. 13). As reconstructed by us, the mylohyoid in the adult attaches ventral to both the middle and posterior mandibular sulci. If Meckel's cartilage occupied both sulci in the adult, then it would have to be dorsal to the full length of the mylohyoid attachment. It is possible that Meckel's cartilage occupied the middle mandibular sulcus and another structure the posterior one, but we deem this unlikely as these two sulci have a faint continuity in the FMNH 28350, are continuous in CM 101007, and are a single structure in the long-nosed armadillo, according to Bensley (1902: fig. 6). Moreover, it is significant that the immature CM 10743 shows no sulci whatsoever, which suggests that the sulcus for Meckel's cartilage present in the fetus is lost postnatally. If not Meckel's cartilage, then what occupied these sulci? In the fetus, a small branch of the lingual nerve and accompanying vein run forward dorsal to the attachment of the mylohyoid. At the level of the gap between the eighth and ninth tooth germs, this nerve is joined by the larger sublingual artery, a branch of the facial artery, which continues forward dorsal to the mylohyoid and geniohyoid attachments (Fig. 13). We believe that these nervous and vascular structures are the most probable occupants of the posterior and middle mandibular sulci in the adult, as well as the anterior sulcus. The tiny foramina associated with all three sulci in FMNH 28350 support a vascular occupant.

If our interpretation of the sulci in the yellow and long-nosed armadillos is correct, does this mean that

Meckel's cartilage is not the occupant of similarly situated, longitudinal grooves in Mesozoic mammals, as suggested by Simpson (1928)? Recently, two Early Cretaceous gobiconodontids, *Repenomamus* and *Gobiconodon*, have been described preserving what is interpreted as an ossified Meckel's cartilage, and it occupies the broad posterior part of a longitudinal sulcus that tapers anteriorly and extends to the mandibular symphysis in some specimens (Wang et al. 2001; Li et al. 2003; Meng et al. 2003). Based on this and the similarity of the sulci across other Mesozoic taxa, Meng et al. (2003) suggest that an ossified Meckel's cartilage was an occupant of at least the posterior part of the longitudinal sulci occurring in many early mammals. Their case in the fossils is compelling, but what remains largely unknown is the function of seemingly similar grooves in extant mammals. Do they resemble the gobiconodontids, with the sulci related somehow to Meckel's cartilage or do they resemble the yellow armadillo, with the sulci apparently related to vascular and nervous structures?

CRANIAL FORAMINA: CONTENTS AND COMPARISONS

As noted in the Introduction, few detailed descriptions of the adult skull of extant armadillos (or other xenarthrans) exist in the literature. None of the descriptions that do exist (e.g., on *Chlamyphorus*, Macalister 1873; on *Tolypeutes*, Murie 1874) contains details of the contents and variations of the major cranial foramina. Because cranial foramina represent an important source for characters employed by morphologists in phylogenetic analyses, we compile below an alphabetical listing of 58 named cranial structures (e.g., foramina, grooves, canals) that represent conduits for soft tissues (e.g., arteries, veins, nerves, muscles). The vast majority of these 58 structures occur in the yellow armadillo and are mentioned in the Descriptions, but a few that do not (e.g., alisphenoid canal, foramen rotundum) are included for the sake of completeness because they are widely distributed in other eutherians. For these 58 structures, we apply either an anglicized name from the fourth edition of the *Nomina Anatomica Veterinaria* (1994) or a name more widely used in the mammalian literature. Appendix 1 includes additional equivalents for many of these structures.

Among extant placentals, the hard-tissue conduits associated with cranial soft tissues are known in the greatest detail for those few forms in which anatomical textbooks have been produced (e.g., humans, domesticated mammals). Of these, we have chosen the dog as our framework for comparison here, because the cranial morphology in the dog is generally not as derived as in humans or in other domesticated mammals and because an excellent textbook of canine anatomy exists (Evans 1993). Therefore, as a starting point of reference for the yellow armadillo condition of each anatomical entry, we

include a description of the condition in the dog or a more appropriate form in the few instances where the structure is lacking in the dog.

In addition to noting the condition of each anatomical entry in the yellow armadillo and the dog, we include observations on the following taxa: an adult dasypodid *Dasypus kappleri* CM 76828; a juvenile and adult bradyrodid *Bradypus variegatus* CM 2180 and 4457; a juvenile and adult myrmecophagid *Tamandua tetradactyla* CM 6340 and 78750, and an adult *T. mexicana* CM 21007; the Eocene palaeonodons *Metacheiromys* sp. YPM-PU 18107, USNM 26132 and 452349, and *M. dasypus* AMNH 11718 (Simpson 1931; Patterson et al. 1992; Gaudin 1995, 2004; Gaudin and Wible 1999); the Oligocene leptictid *Leptictis dakotensis* (Novacek 1986); and the Late Cretaceous eutherian *Zalambdalestes lechei* (Kielan-Jaworowska and Trofimov 1981; Kielan-Jaworowska 1984; Wible et al. 2004). As a rough approximation, following the phylogenetic analysis of Delsuc et al. (2002, 2003) and Gaudin and Wible (in press), structures present in *Euphractus* and *Dasypus* might be present in dasypodids (armadillos) and cingulatan (armored xenarthrans) primitively; structures present in *Bradypus* and *Tamandua* might be present in pilosans (hairy xenarthrans) primitively; and structures present in all four taxa might be present in xenarthrans primitively. The palaeonodont *Metacheiromys* is included as the potential first outgroup to Xenarthra (Patterson et al. 1992; Gaudin 1995, 2004; Szalay and Schrenk 1998), although others (e.g., Rose and Emry 1993; McKenna and Bell 1997; Rose et al., in press) support closer ties between palaeonodons and pangolins. *Leptictis* and *Zalambdalestes* are included as additional outgroups, the former a placental (Novacek 1986) and the latter a basal eutherian, a member of the placental stem lineage (Wible et al. 2004, in press). Figure 18 shows the phylogenetic relationships among these taxa accepted here.

Lastly, we note instances with those entries where a character concerning that structure has been employed in recent phylogenetic analyses that include xenarthran taxa. The reader is referred to those analyses for additional information (e.g., definitions and distributions of character states).

Accessory Palatine Foramen.—In the dog (Evans 1993), one or more minor palatine foramina (=accessory palatine foramina) occur in the horizontal processes of the right and left palatine bones. These connect to the palatine canal, which also connects to the more anteriorly positioned major palatine foramen between the palatine and maxilla, and transmit the accessory palatine nerves off the major palatine nerve to the back of the hard palate. Distinguishing accessory and major palatine nerves is complicated in the yellow armadillo, because there are multiple small foramina in the palatine and maxilla that connect to the palatine canal (Figs. 1B, 2B, 9).

Following the usage in the dog, we identify the small foramina in the palatine or in the lateral palatamaxillary suture as accessory palatine foramina in contrast to those in the maxilla, which we identify as the major palatine foramina. In the yellow armadillo, there are eight or so small foramina in the middle part of the horizontal process of the palatine or in the lateral palatamaxillary suture.

The expansive horizontal process of the palatine of *Dasypus kappleri* CM 76828 is largely devoid of foramina; there is one small accessory palatine foramen in the anterolateral corner. In *Bradypus variegatus* CM 4457, there is a large, anteriorly directed foramen leading into a deep sulcus in the anterior part of the horizontal process of the palatine that must be the major palatine foramen; posterior to this are a dozen or so small foramina that we identify as accessory palatine foramina. The expansive horizontal process of the palatine of *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 90594 has a half dozen or so small, anteriorly directed accessory palatine foramina. *Leptictis dakotensis* (Novacek 1986) has a middle palatine foramen (=accessory palatine foramen of this report) within the horizontal process of the palatine opposite the second upper molar, but there are no such foramina in *Zalambdalestes lechei* (Wible et al. 2004) or apparently in *Metacheiromys*.

Gaudin and Wible (1999, character 11) scored the condition of the palatine foramina in various edentates, noting the presence of multiple foramina in the maxilla and palatine in xenarthrans, and the presence of major and minor palatine foramina in *Metacheiromys*.

Alisphenoid Canal.—In the dog (Evans 1993), the alar canal (=alisphenoid canal) runs through the base of the right and left alisphenoids; its smaller caudal opening transmits the maxillary artery and accompanying vein, and its larger rostral opening transmits the maxillary artery, accompanying vein, and the maxillary nerve. The maxillary nerve enters the alisphenoid canal from the cranial cavity via the foramen rotundum, also in the alisphenoid. In the forms considered in this report, *Leptictis dakotensis* is the only one with an alisphenoid canal; however, unlike the dog, there is no foramen rotundum in the roof of the alisphenoid canal and the maxillary nerve exits the cranial cavity via the sphenorbital fissure (Novacek 1986).

Canal for Auricular Ramus of Vagus.—According to Evans (1993: 982), the auricular ramus of the vagus nerve in the dog “leaves the vagus near the jugular foramen and runs laterally through the petrous temporal bone to join the facial nerve” proximal to the stylomastoid foramen. In the yellow armadillo, there is a canal for the auricular ramus of the vagus that extends from the jugular foramen to the facial canal, proximal to the stylomastoid foramen, and lies between the petrosal and the entotympanic (not visible in the figures).

Rather than a canal, *Dasypus kappleri* CM 76828 has a tiny foramen for the auricular ramus of the vagus that appears to be entirely within the petrosal positioned between the jugular foramen and the stylomastoid foramen. We are uncertain of the course of the auricular ramus of the vagus in *Bradypus variegatus* CM 4457, because it is difficult to see into the depths of the jugular foramen. In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007, there is no visible canal for the auricular ramus of the vagus; the nerve likely passes through the large gap between the jugular fossa and postpromontorial tympanic sinus that is floored by the entotympanic. Similarly, there is no osseous indication of the course of the auricular ramus of the vagus in *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004). The condition in *Metacheiromys* is unknown.

Carotid Foramen, Sulcus, and Canal.—In the dog (Evans 1993), the course of the internal carotid artery across the basicranium is within a perbullar canal (sensu Wible 1986). There are three foramina associated with the artery's course; one at its entrance into the carotid canal, a second at its exit from the canal, and a third at its entrance into the cranial cavity. The associated nomenclature employed by Evans (1993) is confusing and contradictory. Rather than interpret Evans' text, we include the relevant passages here. On page 144, “the carotid canal (canalis caroticus) runs longitudinally through the medial wall of the osseous bulla where it articulates with the basioccipital bone. It begins at the caudal carotid foramen (foramen caroticum caudalis), which is hidden in the depths of the petrobasilar fissure. It runs rostrally, makes a ventral turn at a little more than a right angle, and opens to the outside at the foramen lacerum. At its sharp turn ventrad it concurs with the caudal part of the sphenoid bone, which here forms not only the rostral boundary of the vertical parts of the carotid canal but also the rostral boundary of an opening in the braincase, the internal carotid foramen (foramen caroticum internum).” On page 620, “the artery enters the caudal carotid foramen in the petro-occipital fissure and traverses the carotid canal. On leaving the internal carotid foramen, which is the rostral opening of the carotid canal, it passes ventrally through the foramen lacerum, forms a loop, and re-enters the cranial cavity through the same foramen.” From our reading, Evans (1993) employs two terms for the foramen in the braincase (=carotid foramen of this report): on page 144 internal carotid foramen and on page 620 foramen lacerum. He also uses the term internal carotid foramen in two senses: on page 144 for the foramen in the braincase and on page 620 for the rostral opening of the carotid canal.

The internal carotid artery and accompanying nerves and veins in the yellow armadillo follow an extrabullar course (sensu Wible 1986). The internal carotid

artery runs in a longitudinal sulcus in the medial aspect of the entotympanic (Fig. 4); part of the sulcus anteriorly may be closed to form a short carotid canal (Figs. 9C, E, F). The sulcus or canal leads to the carotid foramen (Fig. 4) in the skull base between the basisphenoid, petrosal, entotympanic (underlying the petrosal), and in some instances the tympanic process of the pterygoid (underlying the basisphenoid).

In *Dasypus kappleri* CM 76828, there is no carotid sulcus or canal, and the carotid foramen lies between the basisphenoid and petrosal, confluent laterally with the piriform fenestra and posteromedially with the basicochlear fissure and jugular foramen. Wible (1984) reported an extrabullar course, outside the fibrous medial bullar wall, for *Dasypus novemcinctus*. *Bradypus variegatus* CM 4457 has an extrabullar carotid sulcus in the medial aspect of the entotympanic that leads to the carotid foramen between the basisphenoid, petrosal, and entotympanic (underlying the petrosal). In other *Bradypus*, the entotympanic typically forms a short carotid canal proximal to the carotid foramen (Patterson et al. 1992; Gaudin 1995). In contrast to the extrabullar course in armadillos and the sloth, the internal carotid artery in *Tamandua mexicana* CM 21007 is within a deep, longitudinal sulcus on the promontorium of the petrosal in the middle ear, a transpromontorial course (sensu Wible 1986); the carotid foramen is entirely within the basisphenoid. In *Metacheiromys*, the internal carotid artery travels in a longitudinal sulcus along the medial surface of the posterior half of the entotympanic, perforating that bone about midway along its length (Patterson et al. 1992; Gaudin 1995). The further course of the artery is unclear. The promontorium in *Metacheiromys* lacks a transpromontorial sulcus. The internal carotid likely follows either a peribullar course or an intratympanic course medial to the promontorium, where it presumably enters the braincase through a carotid foramen that is hidden from view ventrally by the ossified bulla (Patterson et al. 1992; Gaudin 1995). In the Paleocene palaeonodont *Palaeonodon*, however, the carotid perforates the bulla posteriorly and travels across the promontorium of the petrosal in a well-developed sulcus, ending in a carotid foramen surrounded by the petrosal, basisphenoid, and entotympanic (Patterson et al. 1992; Gaudin 1995). *Leptictis dakotensis* also has a transpromontorial groove for the internal carotid; its carotid foramen is between the basisphenoid and petrosal (Novacek 1986). *Zalambdalestes lechei* has a carotid foramen and sulcus entirely within the basisphenoid and, therefore, likely has an extrabullar course for the internal carotid artery (Wible et al. 2004).

MacPhee (1994: character 17) used the extracranial course of the internal carotid artery (i.e., transpromontorial, peribullar, and extrabullar) as a character. Gaudin (1995) used three characters involving the course of the internal carotid artery and the nature of the carotid foramen: character 15, carotid foramen fully exposed, partial-

ly or fully covered ventrally by the entotympanic and ectotympanic; character 26, degree of entotympanic participation in the wall of the sulcus for the internal carotid artery; and character 67, presence of an internal carotid artery foramen (=carotid canal) within the entotympanic or between the entotympanic and basicranium. Gaudin and Branham (1998: characters 39 and 43) used the position of the internal carotid artery relative to the entotympanic (medial or dorsal) and the presence of a transpromontorial sulcus in *Tamandua* and *Myrmecophaga* as characters. Gaudin and Wible (1999: character 27) also used the course of the internal carotid artery as a character in their study.

Caudal Palatine Foramen.—In the dog (Evans 1993), the caudal palatine foramen for the major palatine nerve and artery is within the perpendicular lamina of the right and left palatines posteroventral to and separated by a narrow septum from the sphenopalatine foramen. In the yellow armadillo, the comparable foramen lies between the maxilla and palatine and is confluent with the smaller, more anterodorsally placed sphenopalatine foramen, although some separation of the two foramina occurs in FMNH 28350 (Fig. 3B) and CM 61426. Three separate canals are visible within the floor of the caudal palatine foramen: from anterior to posterior, based on the fetus, these are for the major palatine nerve and vessels (visible in the fetus in Fig. 14), a vein, and the minor palatine nerve and vessels (the posterior two are visible in the adult in Fig. 3B). Consequently, the caudal palatine foramen of the yellow armadillo is not strictly homologous with that in the dog; it includes the caudal palatine foramen and the notch in the back of the palate associated with the minor palatine nerve and artery of the dog.

In the remaining xenarthrans examined, but not in the outgroups, the caudal palatine foramen resembles that in the yellow armadillo in that it appears to transmit both the major and minor palatine nerves and vessels. In *Dasypus kappleri* CM 76828, the caudal palatine and sphenopalatine foramina are confluent, located between the palatine, pterygoid, and ethmoid on the right side and between the pterygoid and ethmoid on the left. In *Bradypus variegatus* CM 4457, the caudal palatine and sphenopalatine foramina are separated from each other; both are in the palatine, but the former is centrally placed and the latter is anterodorsal. A single caudal palatine foramen occurs on the specimen's left side, but on the right are two openings, presumably for the major and minor palatine nerves, respectively. In *Tamandua tetradactyla* CM 78750, the caudal palatine and sphenopalatine foramina occupy a common depression in the palatine, but are separated by a stout septum; the caudal palatine foramen is posterior to the sphenopalatine foramen. *Tamandua mexicana* 21007 differs in the arrangement of the internal openings of the caudal palatine foramen; the opening for the major palatine nerve is

in a common depression with the sphenopalatine foramen, separated by a thin septum, whereas the opening for the minor palatine nerve is separated from these by a stout septum. In *Metacheiromys* sp. YPM-PU 18107, there is a large, round, matrix-filled foramen between the palatine and the frontal that almost certainly houses the openings for the sphenopalatine and caudal palatine foramina, but the specimen would require further preparation to determine whether these openings were separate or confluent. In *Leptictis dakotensis*, Novacek (1986) reported the caudal palatine and sphenopalatine foramina as confluent between the palatine and orbitosphenoid, but Asher (1999) observed separate openings for these in the orbital wall (see also, Novacek 1986: figs. 9, 11). In *Zalambdalestes lechei* (Wible et al. 2004), the caudal palatine and sphenopalatine foramina are confluent, between the palatine, frontal, and maxilla in the latter.

Dasypus kappleri CM 76828 has an anteriorly directed foramen situated immediately anteroventral to and continuous with the confluent caudal palatine/sphenopalatine foramina. Because of the continuity, the occupant of this unusual foramen must pass through the confluent caudal palatine/sphenopalatine foramina. It is within the palatine on the right and between the palatine and pterygoid on the left. We are uncertain of the function of this foramen, which is actually larger than the confluent caudal palatine/sphenopalatine foramina, and report that it is not present in any of the CM specimens of *Dasypus novemcinctus*.

Cavum Supracochleare.—The cavum supracochleare of Voit (1909) is the extradural space occupied by the sensory geniculate ganglion of the facial nerve. Usually in therians (Wible 1990), the cavum supracochleare is separated by the petrosal bone from the back of the cavum epiptericum of Gaupp (1908), the extradural space occupied by the trigeminal ganglion. The dog shows the usual therian condition with the geniculate ganglion enclosed within what is termed the genu of the facial canal within the petrosal (Evans 1993). In contrast, the cavum supracochleare of the yellow armadillo does not have a bony floor and, therefore, is visible within the middle ear (Fig. 4C).

As in the yellow armadillo, *Dasypus kappleri* CM 76828 has no bony floor to the cavum supracochleare. In *Bradypus variegatus* CM 22556, the cavum supracochleare is not separated by bone from the cavum epiptericum and is visible from within the cranial cavity; it does have a bony floor and is not visible from within the middle ear. In *Tamandua mexicana* CM 21007, the cavum supracochleare is enclosed within the petrosal as it is in *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004). In *Metacheiromys*, the condition is unknown, although in the Paleocene *Palaeonodon* the cavum supracochleare is apparently within the petrosal (Patterson et al. 1992).

Cochlear Canaliculus.—In the dog (Evans 1993), the paired perilymphatic ducts enter the right and left petrosal bones via the external opening of the cochlear canaliculus, which is in the rostral edge of the jugular foramen. In contrast, in the yellow armadillo, the cochlear canaliculus is more dorsally placed and is not visible in the jugular foramen (visible in the fetus in Fig. 17).

The remaining xenarthrans examined exhibit the canine condition: *Dasypus kappleri* CM 76828, *Bradypus variegatus* CM 4457, *Tamandua tetradactyla* CM 78750, and *T. mexicana* CM 21007. *Leptictis dakotensis* also has the canine condition for its cochlear canaliculus (=aqueductus cochleae of Novacek 1986), and the condition in *Metacheiromys* and *Zalambdalestes lechei* is unknown.

Gaudin and Wible (in press: character 148) used the position of the cochlear canaliculus, either opening in the jugular foramen or in the cranial cavity, as a character.

Craniopharyngeal Canal.—According to Evans (1993: 139), in the basisphenoid of the dog, “occasionally the small craniopharyngeal canal...persists in the adult, particularly in Bulldogs. This midline canal is a remnant of the pharyngeal diverticulum to the hypophyseal fossa from which the pars glandularis of the hypophysis develops.” A small craniopharyngeal canal through the basisphenoid is preserved in all examined specimens of the yellow armadillo; it is on the midline, closer to the anterior border of the basisphenoid than to the posterior one (Figs. 2B, 9).

Dasypus kappleri CM 76828, *Tamandua tetradactyla* CM 91944, *T. mexicana* CM 21007, *Metacheiromys* (YPM-PU 18107; Simpson 1931), *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* (Wible et al. 2004) have no remnant of the craniopharyngeal canal. *Bradypus variegatus* CM 2180 and 4457 has a tiny opening that appears not to pierce through the basisphenoid, very near that bone’s anterior border, but we cannot exclude this as a remnant of the craniopharyngeal canal.

Dorsal Condylloid Foramen.—In the dog (Evans 1993), the dorsal condylloid fossa is a depression on the occiput above each occipital condyle in the exoccipital bones; foramina are not reported or illustrated within this fossa. In the yellow armadillo, two or three small nutrient foramina that we identify as dorsal condylloid foramina open into the dorsal condylloid fossa (Fig. 5).

Dorsal condylloid foramina are absent in *Dasypus kappleri* CM 76828. Two tiny foramina are present in *Bradypus variegatus* CM 4457, and two tiny ones occur on one side and one on the other side in *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007. None is described or figured for *Metacheiromys* (Simpson 1931) or *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* has a tiny foramen on the left side only (Wible et al. 2004). The Paleocene

Palaeonodon sp. USGS 21876 also has a dorsal condyloid foramen on the left side only.

Ethmoidal Foramen.—The dog has two ethmoidal foramina per side, a larger posterodorsal one in the orbital process of the frontal for the external ethmoidal artery and companion vein, and a smaller anteroventral one in the suture between the frontal and orbitosphenoid for the ethmoidal nerve; sometimes these two foramina are confluent (Evans 1993). The yellow armadillo also has two ethmoidal foramina (Fig. 3B); an anterodorsal one in the frontal for the external ethmoidal vessels and a posteroventral one either in the frontal or between the frontal and orbitosphenoid for the ethmoidal nerve.

Dasypus kappleri CM 76828 has two ethmoidal foramina, posteroventral and anterodorsal, but these are much closer to each other than in the yellow armadillo, and in fact, both foramina are between the ethmoid and the frontal and lead into the same intramural space. Leading into the posteroventral foramen from below and behind is a well-developed sulcus on the ethmoid. *Bradypus variegatus* CM 4457 has only one ethmoidal foramen, which based on the juvenile CM 2180 is entirely within the frontal. *Tamandua tetradactyla* CM 6340 and *T. mexicana* CM 21007 also have only one ethmoidal foramen, between the frontal and the orbitosphenoid. *Metacheiromys* (Gaudin and Wible 1999), *Leptictis dakotensis* (Novacek 1986: ophthalmic foramen in fig. 10), and *Zalambdalestes lechei* (Wible et al. 2004) each have one ethmoidal foramen, between the frontal and the orbitosphenoid in the former two taxa and within the frontal in the last.

Gaudin and Wible (1999: character 16) used the position of the ethmoidal foramen, either within the frontal or between the frontal and the orbitosphenoid, as a character. Gaudin and Wible (in press: character 75) employed the number of ethmoidal foramina as a character.

Facial Canal and/or Facial Sulcus.—In the dog (Evans 1993), the course of the facial nerve through the right and left petrosal bones between the internal acoustic meatus endocranially and the stylomastoid foramen on the skull base is entirely within a bony facial canal. Following MacPhee (1981), we restrict the term facial canal to the bone-enclosed part of the facial nerve course through the middle ear. In the yellow armadillo (Fig. 4C), the anterior half of the tympanic course of the facial nerve, immediately posterior to the cavum supracochleare, is in an open facial sulcus with a high lateral wall, the rostral continuation of the crista parotica; in contrast, the posterior half, anterior to the stylomastoid foramen in the external acoustic meatus, is enclosed in a facial canal. The composition of the facial canal is uncertain. The anterior opening is entirely within the petrosal, whereas the posterior opening is between the petrosal and

ectotympanic; Patterson et al. (1989) report that the tympanohyal contributes to the canal, but do not specify how.

In *Dasypus kappleri* CM 76828 and *Bradypus variegatus* CM 22556, the tympanic course of the facial nerve is entirely within an open facial sulcus; the former has a high lateral wall, the crista parotica, whereas the latter has high medial and lateral walls in its posterior half, the lateral being the crista parotica and the medial being the crista interfenestralis (sensu Wible et al. 1995). In *Tamandua*, the facial sulcus is open for at least part of its course (Guth 1961: fig. 17; see also *Myrmecophaga*, Patterson et al. 1992: fig. 13). In *Metacheiromys*, the facial sulcus is open with a strong lateral wall (Gaudin and Wible 1999). In *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004), the tympanic course of the facial nerve is in an open sulcus with low medial and lateral walls.

Gaudin and Wible (1999: character 30) used the condition of the facial sulcus (open, with weak crista parotica, open with strong crista parotica, or closed canal) as a character.

Foramen for Frontal Diploic Vein.—In the dog (Evans 1993), the frontal diploic vein, an emissary vein of the diploë of the right and left frontal bones to the ophthalmic vein, departs the skull via an unnamed foramen in the orbital surface of the postorbital process of the frontal (for distribution of the frontal diploic vein in other eutherians, see Thewissen 1989). In the yellow armadillo (Fig. 3A), the frontal diploic vein exits via a small, anteroventrally directed foramen that is just below the supraorbital margin of the frontal; this is double on the left side of CM 10743.

Dasypus kappleri CM 76828 and *Bradypus variegatus* CM 2180 have a foramen for the frontal diploic vein that is comparable to that of the yellow armadillo except that it is relatively larger and ventromedially directed. In contrast, in *B. variegatus* CM 4457, there are three smaller, anteroventrally directed foramina in the comparable location. The number also varies in *Tamandua*, in which the foramina are largely anterolaterally directed. In *T. tetradactyla* CM 78750, there are two large foramina and one small foramen with at least one of the larger located just above the supraorbital margin of the frontal; in *T. mexicana* CM 21007, there is one large foramen above the supraorbital margin and an additional small foramen on the left side only below the supraorbital margin. *Metacheiromys* has one small foramen located below the supraorbital crest (Gaudin and Branham 1998; Gaudin 2004). *Leptictis dakotensis* has two small foramina dorsal to the supraorbital margin and visible in dorsal view (Novacek 1986: fig. 6), and foramina are lacking in *Zalambdalestes lechei* (Wible et al. 2004), although a small one is present within the orbit in the slightly older zalambdalestid *Kulbeckia kulbecke* (Arehibald and Averianov 2003).

Gaudin and Branham (1998: character 16) used the position of this foramen with regard to the supraorbital margin as a character, with it dorsal to the supraorbital margin in *Tamandua* and *Myrmecophaga* among xenarthrans. Gaudin (2004: character 176) used the presence or absence of this foramen as a character.

Foramen for Inferior Petrosal Sinus.—In the dog (Evans 1993), the ventral petrosal sinus (=inferior petrosal sinus) drains from the cavernous sinus to the internal jugular vein via the right and left petro-occipital (petrobasilar) canals, between the petrosals and basioccipital. In addition to the inferior petrosal sinus, a condyloid artery off the occipital artery travels in the petro-occipital canal. The caudal opening of the petro-occipital canal (=foramen for the inferior petrosal sinus of this report) lies in the petro-occipital fissure, dorsal to the caudal opening into the carotid canal and anterior to the jugular foramen. In the yellow armadillo (Fig. 4), the foramen for the inferior petrosal sinus is a small, horizontal opening anterior to the jugular foramen between the petrosal, entotympanic, exoccipital, and basioccipital.

In *Dasypris kappleri* CM 76828, the basioccipital and the petrosal are separated by a wide gap, a patent basicochlear fissure, and there is no separate foramen for the inferior petrosal sinus. *Bradypus variegatus* CM 2180, *Tamandua tetradactyla* CM 78750, and *T. mexicana* CM 21007 also do not have a separate foramen for the inferior petrosal sinus, but their basicochlear fissure is closed; the inferior petrosal sinus presumably exits via the jugular foramen. The condition is unknown in *Metacheiromys*, but in the Paleocene *Palaeonodon* there is a groove for the inferior petrosal sinus on the medial surface of the petrosal (Patterson et al. 1992). Patterson et al. (1992) noted that the groove extends toward the jugular foramen, but given the state of preservation of their specimen (USGS 21876), it is impossible to determine whether there was a separate foramen. A separate foramen for the inferior petrosal sinus is present between the petrosal and basioccipital in *Leptictis dakotensis* (Wible et al. 2001), but is lacking in *Zalambdalestes lechei* (Wible et al. 2004).

Foramen Magnum.—In the dog (Evans 1993), the foramen magnum is enclosed between the basioccipital, the paired exoccipitals, and the supraoccipital. The same arrangement can be confirmed in the following juveniles: *Euphractus sexcinctus* CM 10743, *Dasypris novemcinctus* CM 1246, *Bradypus variegatus* CM 2180, and *Tamandua tetradactyla* CM 6340. In *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004), the supraoccipital and exoccipitals clearly contribute to the foramen magnum, and it is likely that the basioccipital does as well, but the sutures between the basioccipital and exoccipitals are fused. The condition in *Metacheiromys* is unknown.

Gaudin and Wible (1999: character 45) used the shape of the foramen (circular or oval transversely) as a character. Gaudin and Wible (in press: character 159) characterized the foramen magnum as either narrow (width less than or equal to half the occiput width) or wide (width greater than half the occiput width) with *Dasypris* and *Tolypentes* the only xenarthrans scored as wide.

Foramen Ovale.—In the dog (Evans 1993), the foramen ovale for the mandibular nerve and a small emissary vein is in the base of the right and left alisphenoids; in the posterolateral border of the foramen ovale, a small notch or even a separate foramen spinosum for the middle meningeal artery may be present. In the yellow armadillo (Fig. 3B), the foramen ovale for the mandibular nerve, accompanying vein, and middle meningeal artery sits in a common depression with the transverse canal foramen in the alisphenoid bone; the foramen ovale is dorsolateral to the transverse canal foramen.

In *Dasypris kappleri* CM 76828, the foramen ovale resembles that of the yellow armadillo; it is posterodorsolateral to and in a common depression in the alisphenoid with the transverse canal foramen. A transverse canal foramen (see below) does not occur in the remaining xenarthrans studied (Gaudin and Wible, in press) or in the xenarthran outgroups. In *Bradypus variegatus* CM 4457, the foramen ovale is between the alisphenoid and the pterygoid; in the juvenile CM 2180, it is between these bones plus the squamosal. In the juvenile *Tamandua tetradactyla* CM 9340, the alisphenoid and pterygoid bones are not distinguished by sutures, but based on its position it is likely within the alisphenoid. In *Metacheiromys* (Rose and Emry 1993; Gaudin et al. 1996) and *Leptictis dakotensis* (Novacek 1986), the foramen ovale is within the alisphenoid, whereas in *Zalambdalestes lechei* it is between the alisphenoid, squamosal, and petrosal (Wible et al. 2004).

Gaudin et al. (1996) discussed the condition of the foramen ovale in xenarthrans and other eutherians at some length. The contributions of the various surrounding bones to the margin of the foramen ovale was coded as a character in Gaudin and Wible (1999: character 21) and Gaudin (2004: character 158).

Foramen for Ramus Superior.—Various extant placentals (Wible 1987) as well as *Leptictis dakotensis* (Rougier et al. 1998) and *Zalambdalestes lechei* (Wible et al. 2004) have a foramen in the roof of the right and left middle ears that transmits the ramus superior of the stapedial artery. In the two fossil taxa, the foramen for the ramus superior is between the petrosal and the squamosal. The fetal yellow armadillo has a remnant of the ramus superior derived from the rostral tympanic artery (ramus inferior) that runs through an opening in the auditory capsule's cartilaginous tympanic roof (the petrosal bone

of the adult); we were not able to confirm the presence or absence of this aperture in the adult. However, if it is present, it is clearly a tiny aperture transmitting an insignificant vessel.

A foramen for the ramus superior in the tympanic roof is absent in *Dasybus kappleri* CM 76828, *Bradypus variegatus* CM 22556, and *Tamandua tetradactyla* (Guth 1961). The condition in *Metacheiromys* is unknown.

MacPhee (1994: character 16) used the position of the foramen for the ramus superior as a character.

Foramen Rotundum.—In the dog (Evans 1993), the foramen rotundum is in the base of the right and left alisphenoids in the roof of the alar canal (=alisphenoid canal); it transmits the maxillary nerve and a small emissary vein that then exit the skull via the rostral opening of the alar canal, along with the major content of the alar canal, the maxillary artery. The exit of the maxillary nerve from the skull is not always associated with the alisphenoid canal; *Zalambdalestes lechei*, for example, has a separate foramen for the maxillary nerve within the alisphenoid posterolateral to the sphenorbital fissure, but no alisphenoid canal (Wible et al. 2004). In general, most authors (e.g., Gregory 1910; McDowell 1958) employ the term foramen rotundum for the separate foramen for the maxillary nerve, and we follow that practice here. In the yellow armadillo, the foramen rotundum and alisphenoid canal are lacking, and the maxillary nerve exits the skull via the sphenorbital fissure (Fig. 3B).

Dasybus kappleri CM 76828 resembles the yellow armadillo in lacking the foramen rotundum (and alisphenoid canal). In contrast, the pilosans examined have a separate foramen rotundum (but no alisphenoid canal). In *Bradypus variegatus* CM 4457, the foramen rotundum is posterolateral to the sphenorbital fissure within the palatine on the right and between the alisphenoid and the palatine on the left. In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 91944, the foramen rotundum is between the palatine and the alisphenoid, hidden in lateral view within a common recess with the sphenorbital fissure. Although Simpson (1931) stated that a separate foramen rotundum is probably absent in *Metacheiromys dasybus* and Gaudin (2004) scored the foramen rotundum as absent in *Metacheiromys*, the foramen rotundum is clearly present in YPM-PU 18107 as a small, separate opening located within the alisphenoid almost midway between the sphenorbital fissure and the foramen ovale (scored correctly in Gaudin and Wible 1999). A separate foramen rotundum is lacking in *Leptictis dakotensis* (Novacek 1986).

MacPhee (1994: character 7), Gaudin and Branham (1998: character 28), Gaudin and Wible (1999: character 19; in press: character 81), and Gaudin (2004: character 159) used the presence of a separate foramen rotundum or its confluence with the sphenorbital fissure as a character. This character has been used by Wetzel (1975) to help

distinguish *Tamandua tetradactyla* and *T. mexicana*, with a separate foramen rotundum present in most (but not all) skulls of *T. tetradactyla* and absent in most (but not all) skulls of *T. mexicana*.

Foramen Stylomastoideum Tertium (Patterson et al. 1989).—The facial nerve has an unusual course in the yellow armadillo and in other euphractines (Patterson et al. 1989). It leaves the right and left middle ear via a stylomastoid foramen between the ectotympanie and the paroccipital process of the petrosal, which in turn opens within the external acoustic meatus. The facial nerve then exits the external acoustic meatus via another foramen, this one being a sizeable gap on the skull base between the ectotympanic and the paroccipital process of the petrosal (Fig. 2B). Patterson et al. (1989) coined the term foramen stylomastoideum tertium for the aperture on the euphractine skull base, to distinguish it from the other two conditions of the stylomastoid foramen that are often encountered in the literature (e.g., MacPhee 1981): the foramen stylomastoideum primitivum, which is the embryonic condition retained in some adults where the facial nerve exits the middle ear for the skull base via a notch formed by the tympanohyal, and the foramen stylomastoideum definitivum, where the facial nerve exits the middle ear for the skull base via a true foramen. None of the other forms examined here has a foramen stylomastoideum tertium.

Foramina for Rami Temporales.—Wible et al. (2004) employed the term subsquamosal foramina for openings in the right and left squamosal bones dorsal to the suprameatal bridge transmitting rami temporales of the stapedial artery and accompanying veins. We follow that terminology here, but the condition in the yellow armadillo is unusual in that most of the foramina for the rami temporales are within the parietal bone (Figs. 1C, 2C, 3A). To avoid confusion, we employ the more general term foramina for rami temporales for these openings, no matter what bone(s) contain them.

The dog has no foramina for rami temporales and the vascular supply to the temporalis muscle follows an entirely extracranial course (Evans 1993). In the yellow armadillo (Figs. 1A, C, 2A, C, 8), the foramina for the rami temporales and accompanying veins are asymmetrically arranged, with about a dozen in the parietal and another dozen or fewer within the squamosal or between the squamosal and the parietal.

In *Dasybus kappleri* CM 76828, the parietal has five foramina on the right side and two on the left; the squamosal has three on the right and two on the left; between the squamosal and parietal are one per side; and between the squamosal and frontal is one on the right side only. In *Bradypus variegatus* CM 4457 are two tiny foramina in the left parietal and one in the right. The condition in *Tamandua* differs from the other forms in that

there are openings in the parietal-squamosal suture that resemble foramina for rami temporales, but which transmit the arteria diploëtica magna into the posttemporal canal (see posttemporal canal below). In addition to these are openings wholly within the parietal or within the squamosal that likely transmit rami temporales. In *T. tetradactyla* CM 78750, the parietal has two foramina on the right and four on the left, and the squamosal has one on the right and two on the left. In *T. mexicana* CM 21007, the parietal has one per side. *Metacheiromys* has a variable number of foramina in the parietal and the squamosal. Simpson (1931: fig. 4) figured seven foramina in the right parietal and three on the left in *Metacheiromys dasypus*, with an additional four foramina in the right and left squamosals. Four of the foramina on the right side are situated very close to the parietal-squamosal suture. In *Metacheiromys* sp. YPM-PU 18107, there are at least two foramina in the parietal, one in the squamosal, and one at the parietal-squamosal suture on the left side. On the right, there are again at least two foramina in the parietal, with two more at the parietal-squamosal suture, but none are evident in the squamosal itself. Foramina for rami temporales are also present in the Paleocene *Palaeonodon* (USGS 21876; five on the left parietal, two on the right). *Leptictis dakotensis* has four foramina in the squamosal (Novacek 1986: fig. 17) and *Zalambdalestes lechei* has two in the squamosal (Wible et al. 2004).

Gaudin and Wible (in press: character 97) used the number of foramina in the parietal as a character.

Foramina in Frontal, Dorsal Surface.—In the yellow armadillo (Figs. 1A, 2A, 8), a half-dozen or so foramina, asymmetrically arranged between the right and left sides, occur in the dorsal surface of the frontal bone, transmitting branches of the external ethmoidal artery and vein. *Dasypus kappleri* CM 76828 is the only other form considered here with such foramina; it has four on the left and three on the right.

Gaudin and Wible (in press: character 94) used the presence/absence of these foramina as a character.

Foramina in Frontal, Temporal Surface.—The yellow armadillo is the only form considered here to have foramina, between two and six, in the right and left temporal surfaces of the frontal bone (Figs. 1A, C, 2A, C, 3A). These foramina transmit temporal rami from the orbitotemporal canal to the temporalis muscle.

Gaudin and Wible (in press: character 95) used the presence/absence of these foramina as a character.

Glaserian Fissure.—According to Klaauw (1931: 164), during ontogeny, the fissura Glaseri forms first in the anterior wall of the presumptive auditory bulla as an aperture for Meckel's cartilage. Meckel's cartilage subsequently disappears and "later on we find the chorda tym-

pani nerve in it and often the ramus inferior of the stapedia artery." As the elements forming the auditory bulla vary among mammals (Klaauw 1931; Novacek 1977), so do the elements forming the Glaserian fissure. In the dog (Evans 1993), the chorda tympani nerve passes through a small canal in the anterodorsal wall of the right and left auditory bullae and emerges through the petrotympanic fissure by a small opening medial to the postglenoid process. In the yellow armadillo (Figs. 4A, B), the Glaserian fissure for the chorda tympani is between the ectotympanic and the squamosal, medial to the entoglenoid process of the squamosal and the anterior process of the malleus, and posterolateral to the foramen ovale.

Dasypus kappleri CM 76828 does not have a bone-enclosed Glaserian fissure; there is a shallow, longitudinal groove in the alisphenoid posterior to the lateral edge of the foramen ovale that likely transmits the chorda tympani nerve. In *Bradypus variegatus* CM 4457, the Glaserian fissure lies between the ectotympanic, squamosal, and pterygoid, well posterolateral to the foramen ovale. In *Tamandua tetradactyla* CM 78750, the Glaserian fissure is even further removed from the foramen ovale, between the squamosal and the alisphenoid, and these bones plus the ectotympanic in *T. mexicana* CM 21007. The Glaserian fissure of *Metacheiromys* sp. YPM-PU 18107 opens into a groove that travels medially behind the entoglenoid process of the squamosal and a flange of the alisphenoid immediately posterior to the foramen ovale. In *Leptictis dakotensis*, the Glaserian fissure is a sulcus in the squamosal between the postglenoid and entoglenoid processes, well posterolateral to the foramen ovale (Novacek 1986). There is no specific impression for the chorda tympani nerve in *Zalambdalestes lechei*; a sulcus on the tegmen tympani of the petrosal housed the ramus inferior of the stapedia artery (Wible et al. 2004) and perhaps the chorda tympani as well, in light of its proximate position to the foramen ovale.

Gaudin (1995: character 14) employed the presence of a distinct groove in the squamosal leading to the Glaserian fissure from behind and medial to the entoglenoid process of the squamosal as a character. Gaudin and Wible (in press: characters 113 and 140) used the presence/absence of an alisphenoid contribution to the Glaserian fissure and the position of the Glaserian fissure and ectotympanic to the foramen ovale as characters.

Hiatus Fallopii.—In the dog (Evans 1993), the greater petrosal nerve runs forward from the geniculate ganglion of the facial nerve within the right and left petrosals in a canal termed the petrosal canal, dorsal to the fossa for the tensor tympani muscle. It exits the petrosal canal at a small aperture near the distal end of the petrosquamous suture. For the opening transmitting the greater petrosal nerve from the petrosal, we employ the term hiatus Fallopii (McDowell 1958). In the yellow

armadillo, the hiatus Fallopii is lacking because the greater petrosal nerve lies in an open sulcus within the middle ear that parallels the lateral edge of the epitympanic wing of the petrosal and anteriorly disappears under cover of the auditory bulla (not visible in the figures). Based on the fetus, we interpret the greater petrosal nerve as exiting the middle ear beneath the piriform fenestra and joining the deep petrosal nerve beneath the carotid foramen to form the nerve of the pterygoid canal.

In *Dasypus kappleri* CM 76828, the petrosal course of the greater petrosal nerve differs on the right and left sides. On the left, it is in an open sulcus within the middle ear as in the yellow armadillo, and, therefore, the hiatus Fallopii is absent. However, on the right side the lateral and medial walls of the sulcus for the greater petrosal nerve abut to form a canal, which retains an open seam where the walls contact ventrally. Consequently, the right side has an anterior opening of the greater petrosal nerve or hiatus Fallopii located just lateral to the anterolateral aspect of the promontorium, within the middle ear. Based on an isolated left petrosal of *Bradypus variegatus* CM 22556, the hiatus Fallopii is absent because the petrosal course of the greater petrosal nerve is entirely in a sulcus within the cranial cavity. In *Leptictis dakotensis* (Rougier et al. 1998) and *Zalambdalestes lechei* (Wible et al. 2004), the hiatus Fallopii is present at the anterior end of the tegmen tympani. The condition in *Metacheiromys* is unknown.

Hypoglossal Foramen.—In the dog (Evans 1993), the hypoglossal foramen, the external opening of the hypoglossal canal, is in the paired exoccipital bones, posterolateral to the jugular foramen; it transmits the hypoglossal nerve and vein. In the yellow armadillo, the hypoglossal foramen is either single or double per side, posterolateral and ventral to the jugular foramen (Figs. 2B, 4A, B). Based on CM 10743 (Fig. 9D), the hypoglossal foramen is entirely within the exoccipital bone and based on the fetus it transmits the hypoglossal nerve, a caudal meningeal branch of the occipital artery, and a vein that joins the inferior petrosal sinus and the sigmoid sinus to form the internal jugular vein.

Dasypus kappleri CM 76828, which does not preserve the basioccipital-exoccipital suture, has one hypoglossal foramen per side, posterolateral and ventral to the jugular foramen; in the juvenile *D. novemcinctus* CM 1246, the single hypoglossal foramen is within the exoccipital. *Bradypus variegatus* CM 4457, which does not preserve the basioccipital-exoccipital suture, has a single hypoglossal foramen, posterolateral to and level with the jugular foramen; in the juvenile CM 2180, the hypoglossal foramina (single on the left, paired on the right) is within the exoccipital. In *Tamandua tetradactyla* CM 6340, the hypoglossal foramen is single, posterolateral to and level with the jugular foramen, and within the exoccipital; the foramen is also single in *T. mexicana*

CM 21007. *Metacheiromys* has a single foramen (Simpson 1931) lying posterior and ventral to the jugular foramen. In *Leptictis dakotensis*, the hypoglossal foramen is single and posterolateral and ventral to the jugular foramen (Novacek 1986); in *Zalambdalestes lechei*, it is double or triple and posterolateral and ventral to the jugular foramen (Wible et al. 2004). None of these fossil taxa preserves the basioccipital-exoccipital suture.

Gaudin (1995: character 66) scored the degree of separation between the jugular foramen and hypoglossal foramen as a character. Gaudin and Branham (1998: character 47) and Gaudin (2004: character 187) used the size of the hypoglossal foramen as a character, and Gaudin and Wible (in press: character 152 and 153) used the position relative to the jugular foramen (ventral or level/dorsal) and number as characters.

Incisive Foramen.—In the dog (Evans 1993), the paired palatine fissures (=incisive foramina) are bean-shaped and just off the midline, largely in the right and left incisive bones (=premaxillae) with the maxillae forming the posterior border; each foramen is longer than the alveolus for the upper canine and transmits the nasopalatine duct connecting the oral and nasal cavities and the vomeronasal organ, the rostral septal branch of the major palatine artery, and the septal branch of the caudal nasal nerve (=nasopalatine nerve). In the yellow armadillo (Figs. 1B, 2B), the incisive foramen is also bean-shaped, but smaller than the smallest upper tooth and entirely within the premaxilla. In the fetus, the anterior part of the incisive foramen transmits the nasopalatine duct and the posterior part of the nasopalatine nerve along with a small companion artery and vein. As in the dog, the nasopalatine duct connects the oral and nasal cavities and the vomeronasal organ.

In *Dasypus kappleri* CM 76828, the incisive foramen is slightly longer than the smallest upper tooth and entirely within the premaxilla on the left, with a very small sliver of maxilla contributing on the right. The premaxillae are not preserved in any CM *Bradypus*. Gaudin (2004: fig. 3B) has a line drawing of a *Bradypus* in ventral view with the premaxillae in place. The elongate incisive foramen is between the premaxilla and maxilla and is more than half the length of the premaxilla. In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 95904, the elongate incisive foramen is largely in the premaxilla, with the maxilla forming the posterior border, and is more than half the length of the premaxilla. The incisive foramen of *Metacheiromys* sp. YPM-PU 18107 is small, much less than half the anteroposterior length of the palatal process of the premaxilla and only slightly larger than the alveoli for the peg-like postcanines. It is well separated from the midline, and is surrounded by the premaxilla except for its posterior edge, which is formed by the maxilla. In *Leptictis dakotensis*, the incisive foramen is largely in the premaxilla, with the maxilla forming

the posterior border, and is roughly the length of the ultimate upper incisor alveolus (Novacek 1986). In *Zalambdalestes lechei*, the incisive foramen is very small, nearer the alveolar border than the midline, and facing posteromedioventrally (Wible et al. 2004).

Gaudin (2004: character 117) examined variation in the shape of the incisive foramen. Gaudin and Wible (1999: character 5) used the osseous elements contributing to the incisive foramen as a character. Gaudin and Wible (in press: character 52) also used the latter character, scoring the size of the incisive foramen (character 53) as well.

Infraorbital Canal.—In the dog (Evans 1993), the infraorbital canal carries the infraorbital nerve, artery, and vein from the right and left orbit to the snout. The anterior opening of each infraorbital canal on the snout, the infraorbital foramen, is within the maxilla, and the posterior opening in the orbit, the maxillary foramen, is between the maxilla, lacrimal, and jugal. The infraorbital canal is roughly the same length as the enlarged upper carnassial tooth, the ultimate upper premolar. In the yellow armadillo (Figs. 3A, 10), the infraorbital canal, entirely within the maxilla, transmits the same structures as in the dog and is less than the length of two teeth.

In *Dasypus kappleri* CM 76828, the infraorbital canal is slightly more than the length of two teeth; it is almost entirely in the maxilla, with a small contribution from the palatine to the posterodorsal roof. In *Bradypus variegatus* CM 4457, the infraorbital canal is shorter than the length of one tooth; it is almost entirely in the maxilla, with a tiny contribution from the lacrimal to the posterodorsal roof. Oddly enough, the infraorbital canal is absent bilaterally in *B. variegatus* CM 1492; and the infraorbital nerve and vessels must run under the zygomatic process of the maxilla. In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 90594, the infraorbital canal is largely in the maxilla with contributions from the palatine and the lacrimal posterodorsally (except on the right side of the latter in which the lacrimal is excluded) and is comparable in length to that in *D. kappleri* CM 76828. The infraorbital canal of *Metacheiromys* sp. YPM-PU 18107 is entirely within the maxilla, and is more than one and a half times longer than the anteroposterior length of the enlarged canine alveoli. In *Leptictis dakotensis*, the infraorbital canal is within the maxilla and roughly the length of the upper first or second molar (Novacek 1986: fig. 7). In *Zalambdalestes lechei*, the infraorbital canal is largely in the maxilla with a contribution from the lacrimal posterodorsally and is more than the length of the first and second upper molars (Wible et al. 2004).

Gaudin (2004: character 156) used the position and length of the infraorbital canal as a character.

Infraorbital Foramen.—In the dog (Evans 1993), the infraorbital foramen within the right and left maxillae

on the snout is the anterior opening of the infraorbital canal transmitting the infraorbital nerve, artery, and vein; it is dorsal to the penultimate upper premolar and not visible in ventral view. In the remaining specimens examined, the infraorbital foramen is invariably within the maxilla. The infraorbital foramen of the yellow armadillo transmits the same structures as in the dog; it is dorsal to the front of the fifth maxillary tooth and is visible in ventral view (Figs. 1B, 2B).

In *Dasypus kappleri* CM 76828, the infraorbital foramen is dorsal to the back of the last maxillary tooth and is visible in ventral view. In *Bradypus variegatus* CM 2180 and 4457, the infraorbital foramen is dorsal to the back of the second maxillary tooth and is visible in ventral view; the foramen and canal are absent in CM 1492. In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007, the infraorbital foramen is visible in ventral view, but cannot be aligned with a tooth position because these forms are edentulous. The infraorbital foramen is not visible in ventral view in *Metacheiromys* (Gaudin 2004). It is situated midway between the two postcanine alveoli in YPM-PU 18107, in the back one-third of the preorbital region. Simpson (1931) illustrated the foramen in a similar position in *M. dasypus*, except that the foramen lies posterior to the sole postcanine alveolus. The infraorbital foramen is hidden from view ventrally in both *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004). It is dorsal to the first upper molar in the former and to the embrasure between the penultimate and more mesial upper premolars in the latter.

Gaudin (2004: character 157) and Gaudin and Wible (in press: character 46) used the visibility of the infraorbital foramen in ventral view as a character.

Jugular Foramen.—In the dog (Evans 1993), the jugular foramen is between the right and left petrosals and the occipital; based on the disarticulated skull of a puppy (Evans 1993: fig. 4–45), it appears to be largely or wholly the exoccipital bone that borders the jugular foramen. After exiting through the jugular foramen, its contents, the glossopharyngeal, vagus, and accessory nerves and the sigmoid sinus, then pass through the petro-occipital and tympano-occipital fissures to reach the skull base. In the yellow armadillo (Fig. 4), the jugular foramen lies between the exoccipital and the petrosal, based on the juvenile CM 10743, which preserves the exoccipital-basioccipital suture (Fig. 9D). The glossopharyngeal, vagus, and accessory nerves exit the anterior part of the jugular foramen, and the caudal meningeal branch of the occipital artery and the sigmoid sinus exit from the posterior part.

In *Dasypus kappleri* CM 76828, the jugular foramen is confluent with the basicochlear fissure; the resulting large gap is bordered by the fused basioccipital-exoccipital medially and the petrosal laterally.

In *Bradypus variegatus* CM 2180 and *Tamandua tetradactyla* CM 6340, the jugular foramen is between the exoccipital and the petrosal. The basioccipital-exoccipital suture is fused in *Metacheiromys*, *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* (Wible et al. 2004). In *Metacheiromys* sp. YPM-PU 18107, the jugular foramen lies between the occipital, petrosal, and entotympanic. In *Leptictis* and *Zalambdalestes*, it is between the occipital and petrosal.

Gaudin (1995) included three characters pertaining to the jugular foramen. The first, character 63, concerns the size of the opening (small or enlarged), the second, character 64, its shape (circular or oval), and the third, character 65, its position relative to the petrosal bone.

Lacrimal Fenestra.—In the dog (Evans 1993: 1041), one of the extraocular muscles, the musculus obliquus ventralis (inferior of this report), “originates from a small depression in the palatine bone near the junction of the palatomaxillary and the palatolacrimal sutures. In prepared skulls this site may appear as a foramen, since the attachment plate is thin and easily lost.” In the yellow armadillo, all examined specimens have an opening in the juncture of the lacrimal, frontal, and maxilla (Fig. 3A). Passing through this opening in the sectioned fetus is the inferior oblique muscle, which originates from the back of the cartilaginous nasal capsule. For the opening in the dog and yellow armadillo, we employ the term lacrimal fenestra, which Jollie (1968: fig. 14) used for what appears to be the same structure in the pangolin orbit, although he did not discuss its contents.

The lacrimal fenestra is absent from the remaining specimens examined with one exception. In *Tamandua*, there is a pit in the palatine near the lacrimal that in some specimens is open as a lacrimal fenestra (e.g., *T. tetradactyla* 78750; *T. mexicana* 76827). Novacek (1986: 37) reported two small pits for the inferior oblique muscle in the lacrimal near the suture with the maxilla for *Leptictis dakotensis*.

Gaudin and Wible (1999: character 15; in press: character 50) used the presence/absence of the lacrimal fenestra as a character.

Lacrimal Foramen.—In the dog (Evans 1993), there is a large opening in the center of the right and left orbital processes of the lacrimal, called the fossa for the lacrimal sac. The lacrimal sac is formed by the union of the two lacrimal ducts, one from each eyelid, and in turn leads into the lacrimal canal, which transmits the nasolacrimal duct forward to the nasal vestibule. In the yellow armadillo, we use the term foramen lacrimale from the Nomina Anatomica Veterinaria (1994) for the anteromedially directed opening in the lacrimal for the nasolacrimal duct. In the specimens examined by us, only one lacrimal foramen per side appears just posterior to the orbital margin (Fig. 3) except on the right side of FMNH

28350, in which this foramen is divided by a thin osseous septum.

In *Dasypus kappleri* CM 76828, a single, anteroventrally directed lacrimal foramen appears on the facial process of the lacrimal, just anterior to the orbital margin. In *Bradypus variegatus* CM 4457, a single, medially directed lacrimal foramen appears in the center of the small facial process of the lacrimal. In *Tamandua tetradactyla* CM 6340 and 78750 and *T. mexicana* CM 90594, two ventrally directed lacrimal foramina appear in the facial process of the lacrimal, just anterior to the orbital margin; the smaller dorsal one leads into the larger ventral foramen. In contrast, in *T. mexicana* CM 21007, there is only one foramen, the equivalent of the larger ventral foramen of the other specimens. *Metacheiromys* sp. YPM-PU 18107 has a single, anterodorsomedially directed lacrimal foramen on the facial process of the lacrimal immediately anterior to the orbital rim. In *Leptictis dakotensis*, a single, anteriorly directed lacrimal foramen is centrally placed in the orbital process of the lacrimal (Novacek 1986) and *Zalambdalestes lechei* has two lacrimal foramina in its orbital process (Wible et al. 2004).

MacPhee (1994: character 5) used the position of the lacrimal foramen relative to the orbital rim as a character. Gaudin and Branham (1998: character 12) used the number and size of the lacrimal foramina as a character. Gaudin and Wible (1999: character 14) combined the absence/presence of the lacrimal bone and lacrimal foramen into a single character (both present, bone present, foramen absent, both absent). Gaudin (2004) used the number of lacrimal foramina (character 141), the size of the lacrimal foramen (character 142), and the absence/presence of prominent lateral walls around the lacrimal foramen (character 144) as characters.

Major Palatine Foramen.—In the dog (Evans 1993), the major palatine nerve and artery enter the caudal palatine foramen in each orbit, pass through the palatine canal in the palatine bone, and exit onto the hard palate via the major palatine foramen between the maxilla and the palatine opposite the distal part of the fourth upper premolar. In the yellow armadillo (Figs. 1B, 2B, 9), in place of a single large major palatine foramen, there are some three dozen small foramina in the maxilla (and the palatine, see accessory palatine foramen above) that transmit branches of the major palatine nerve and vessels.

Dasypus kappleri CM 76828 has more than three dozen small foramina in the maxilla for the major palatine nerve and vessels. *Bradypus variegatus* CM 4457 has a single, large major palatine foramen in the palatine opposite the last upper tooth that leads into a deep, anteriorly directed sulcus extending nearly the length of the maxilla; in addition, within this sulcus and medial and lateral to it are dozens of small foramina in the maxilla. *Tamandua tetradactyla* CM 78750 has dozens of tiny

foramina in the maxilla and one small foramen near the anterior tip of the maxilla that has a sulcus extending anteriorly from it. *Metacheiromys* has a single major palatine foramen located in the anterior palatine or at the palatomaxillary suture (Gaudin and Wible 1999). *Leptictis dakotensis* has one major palatine foramen in the palatine, near the palatomaxillary suture, opposite the ultimate upper premolar, leading into an anteriorly directed sulcus that runs nearly the length of the maxilla (Novacek 1986). *Zalambdalestes lechei* has two major palatine foramina opposite the ultimate and penultimate upper premolars, entirely within the maxilla (Wible et al. 2004).

Mandibular Foramen.—In the dog (Evans 1993), the mandibular foramen is the caudal opening of the mandibular canal for the inferior alveolar nerves and vessels; it is located on the medial side of the mandibular ramus, roughly in the anterior-posterior center, below the alveolar plane of the mandibular dentition. In the yellow armadillo (Fig. 7B), the mandibular foramen is also on the mandibular ramus, roughly in the anterior-posterior center, at the alveolar plane of the mandibular dentition.

In *Dasyops kappleri* CM 76828, the mandibular foramen is well posterior to the last mandibular tooth, anterior to the main part of the coronoid process, and roughly at the alveolar plane. In *Bradypus variegatus* CM 4457, the mandibular foramen is ventral to the tallest part of the coronoid process and roughly at the alveolar plane. In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007, the mandibular foramen is anterior to the main part of the low coronoid process and roughly in the dorsal-ventral center of the mandibular ramus. The foramen is beneath the midpoint of the well-developed coronoid process in *Metacheiromys* sp. YPM-PU 18107, and well below the alveolar margin. In the leptictid *Gypsonictops hypoconus*, the mandibular foramen is located posterior to the main coronoid process, below the alveolar plane (Clemens 1973), and in *Zalambdalestes lechei*, it is anterior to the main part of the coronoid process, below the alveolar plane (Kielan-Jaworowska and Trofimov 1981).

Gaudin and Wible (in press: character 31) used the distance of the mandibular foramen from the back of the tooth row as a character.

Mandibular Sulci.—With the exception of the juvenile CM 10743, the yellow armadillos examined have faint, narrow longitudinal sulci on the lingual surface of each mandibular body. In FMNH 28350 (Fig. 7B), there are anterior, middle, and posterior sulci, each of which contains one or more tiny foramina. The anterior sulcus lies roughly halfway between the dorsal and ventral margins of the mandibular body and extends from the posterior edge of the mandibular symphysis to below the front of the sixth tooth. The middle sulcus lies in a plane ven-

tral to the anterior sulcus, extending from the gap between the fifth and sixth teeth to the middle of the eighth tooth. The posterior sulcus appears to be in the same plane as the middle sulcus, extending from the back of the ninth tooth onto the mandibular ramus, ventral to the mandibular foramen. In CM 6398 and 101007, there is a single longitudinal sulcus extending the same distance as the three in FMNH 28350. CM 6399 has the middle and posterior sulci only, and their path is somewhat different from those in FMNH 28350. The anterior sulcus extends back from the level of the fifth or sixth tooth position to the mandibular foramen, whereas the middle sulcus extends from the middle of the fifth tooth to the posterior edge of the seventh tooth. Bensley (1902: fig. 6) illustrated a sulcus in *Dasyops novemcinctus* (= *Tatania novemcincta*) in the position of the middle and posterior sulci of FMNH 28350 and suggested it contains Meckel's cartilage. Based on the fetal yellow armadillo, nerves and vessels, not Meckel's cartilage, are the most likely occupants of the sulci present in the adults.

Of the other specimens examined here, only *Bradypus variegatus* CM 1492 and 4457 has a faint, narrow longitudinal sulcus under the ultimate mandibular tooth; on the right side of CM 1492, this extends back to just below the mandibular foramen.

Mastoid Foramen.—In the dog (Evans 1993), the mastoid foramen occurs on the right and left sides of the occiput between the exoccipital, the supraoccipital, and the mastoid process (=mastoid exposure of the petrosal of this report); it transmits the occipital emissary vein, which drains the deep muscles on the cranial part of the neck into the sigmoid sinus. Evans (1993: 608) also reports a caudal meningcal artery off the occipital artery that "goes through the supramastoid foramen and ramifies in the dura of the occipital cranial fossa." The supramastoid foramen is not mentioned elsewhere in the text, and we speculate that it may in fact be the mastoid foramen. In the yellow armadillo, the mastoid foramen is lacking (Fig. 5).

A mastoid foramen is lacking from the other xenarthrans examined here. It is not known whether a mastoid foramen is present in *Metacheiromys*, but *Palaeonodon* sp. USGS 21876 has a small mastoid foramen on the medial side of the mastoid exposure of the petrosal. *Leptictis dakotensis* has a mastoid foramen at the junction of the parietal, supraoccipital, and mastoid exposure of the petrosal (Novacek 1986), and *Zalambdalestes lechei* has two mastoid foramina within the mastoid exposure of the petrosal (Kielan-Jaworowska 1984; Wible et al. 2004).

Maxillary Foramen.—In the dog, the maxillary foramen, the posterior opening of the infraorbital canal, is in the anteroventral part of each orbit and transmits the infraorbital nerve and vessels. It is largely in the max-

illa, dorsal to the posterior root of the ultimate upper premolar, with contributions in the roof from the lacrimal and the jugal. In the yellow armadillo, the maxillary foramen transmits the same structures as in the dog and is entirely within the maxilla, dorsal to the sixth maxillary tooth (Fig. 3A). It is not visible in ventral view (Figs. 1B, 2B, 9).

In *Dasybus kappleri* CM 76828, the maxillary foramen is largely within the maxilla, with a small wedge of the ethmoid in the medial wall, well posterior to the ultimate maxillary tooth; it is visible in ventral view. In *Bradypus variegatus* CM 4457, the maxillary foramen is largely within the maxilla, with a small contribution from the jugal to the roof; it is dorsal to the third of five maxillary teeth and is visible in ventral view. In *B. variegatus* CM 1492, the maxillary foramen and infraorbital canal are absent. In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007, the maxillary foramen is between the palatine, maxilla, and lacrimal, and is visible in ventral view. The maxillary foramen of *Metacheiromys* sp. YPM-PU 18107 is situated far behind the end of the reduced postcanine dentition. It is contained entirely within the maxilla (Gaudin 2004), and is not visible in ventral view. In *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004), the maxillary foramen is not visible in ventral view. It is within the maxilla, dorsal to the second upper molar, in the former, and between the maxilla and the lacrimal, dorsal to the first upper molar in the latter.

Gaudin (2004: character 110) used the absence/presence of jugal participation in the rim of the maxillary foramen as a character. Gaudin and Wible (in press: character 63) used the visibility of the maxillary foramen in ventral view as a character.

Mental Foramen.—The dog has two or more mental foramina per side below the anterior lower premolars that transmit the mental nerves, arteries, and veins (Evans 1993). The yellow armadillo has between two and four mental foramina that are below the third, fourth, and fifth lower teeth (Figs. 7A, 10); the sectioned fetus has three foramina, with the anteriormost one transmitting mental nerve, artery, and vein and the other two transmitting only mental nerve and vein.

In *Dasybus kappleri* CM 76828, there is a large anterior mental foramen below the first lower tooth on the left and between the first and second lower teeth on the right, a small middle mental foramen below the second tooth on the left and below the third tooth on the right, and a small posterior mental foramen below the anterior part of the fourth tooth. In *Bradypus variegatus* CM 4457, there is one foramen just off the midline, mesial to the first lower tooth (double on the right). In *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007, there is one large mental foramen leading into a deep sulcus near the anterior tip of the mandible. Simpson

(1931) illustrated only a single large mental foramen in *Metacheiromys dasybus*, situated between the alveoli for the first and second postcanines. However, *Metacheiromys* sp. YPM-PU 18107 has three mental foramina: a small foramen anterior to the large canine tooth, and two larger foramina that lie posterior to the canine but anterior to the single postcanine alveolus. *Leptictis dakotensis* and *Zalambdalestes lechei* have two mental foramina: in the former below the diastemata between the first and second lower premolars and between the second and third lower premolars (Novacek 1986), and in the latter below the first and third lower premolars (Kielan-Jaworowska and Trofimov 1981).

Gaudin and Wible (in press: character 15) used the number of mental foramina as a character.

Minor Palatine Foramen.—In the dog (Evans 1993), the minor palatine nerve and artery arise in each orbit and reach the palate by passing through a deep notch between the palatine and maxilla in the posterior edge of the hard palate that rarely is closed to form a foramen. In the yellow armadillo (Fig. 3B), the minor palatine nerve and vessels enter the large opening in the orbit between the maxilla and the palatine that we identify as the caudal palatine foramen. Within the caudal palatine foramen, the minor palatine nerve and vessels enter the posteriormost of three canals, which leads to the two or three small, posteriorly directed minor palatine foramina on the back of the horizontal process of the palatine (Figs. 1B, 2B).

It appears that the orbital course of the minor palatine nerve and vessels in the remaining xenarthrans resembles that in the yellow armadillo, starting with either a separate caudal palatine foramen or one fused with the sphenopalatine foramen; this appears not to be the case in the outgroups. The subsequent course of the minor palatine nerve and vessels is unclear in *Dasybus kappleri* CM 76828, because there are few foramina in the extensive horizontal process of the palatine; candidates include a half-dozen or so minute foramina just off the midline and one tiny one near the lateral margin. *Bradypus variegatus* CM 4457 has a half dozen small foramina in its very narrow horizontal process of the palatine, posterior to the major palatine foramen. *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007 have a small, posteriorly directed foramen in the posterior third of the horizontal process of the palatine. *Metacheiromys* sp. YPM-PU 18107 has a minor palatine foramen in the posterior palatine. *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004) have a large minor palatine foramen through the very back of the hard palate that is within the palatine in the former and between the palatine, maxilla, and pterygoid in the latter.

Musculotubal Canal.—In the dog (Evans 1993), the auditory tube (Eustachian tube) leaves the right and

left middle ear via the musculotubal canal between the auditory bulla and the alisphenoid; accompanying the auditory tube is the tensor veli palatini muscle. In the yellow armadillo (Fig. 2B), the small, round, medially directed musculotubal canal is in the anteromedial bullar wall between the entotympanic and ectotympanic and transmits only the auditory tube.

A musculotubal canal is absent in those forms in our sample lacking an auditory bulla, i.e., *Dasyurus kappleri* CM 76828 and *Zalambdalestes lechei* (Wible et al. 2004). In *Bradypus variegatus* CM 22556, the musculotubal canal resembles that in the yellow armadillo; it is situated in the anteromedial bullar wall between the entotympanic and ectotympanic. The musculotubal canal in the tamandua differs in that it sits in the medial bullar wall and is ventromedially and slightly posteriorly directed (Patterson et al. 1992; Gaudin 1995); it lies between the ectotympanic and basioccipital in *Tamandua mexicana* 21007 and between those bones and the pterygoid in *T. tetradactyla* CM 6340. The musculotubal canal emerges between the entotympanic, ectotympanic, and alisphenoid in *Metacheiromys* sp. YPM-PU 18107. In *Leptictis dakotensis*, the musculotubal canal is in the anteromedial bullar wall, between the entotympanic and the basisphenoid (Novacek 1986).

Gaudin (1995: characters 62 and 61) and Gaudin and Branham (1998: character 33 and 34) used the orientation and elements bordering the Eustachian tube opening as characters. In addition, Gaudin (1995: character 60) coded the position of the Eustachian tube opening as lying in either the anteromedial or posteromedial corner of the tympanic cavity.

Nasal Foramen.—Simpson (1937) noted two pairs of foramina on the dorsal surface of each nasal bone in the multituberculate *Ptilodus* and suggested a vascular function. Wible and Rougier (2000) suggested that they might have transmitted branches of the ethmoidal nerve and external ethmoidal artery from within the nasal cavity onto the snout. Some of the yellow armadillos examined here have small foramina on the dorsal surface of the nasal (Figs. 1A, 2A, 8), but unlike those in some multituberculates and various other Mesozoic mammaliaforms, these do not appear to penetrate into the nasal cavity and likely transmit nutrient veins, as in the fetal yellow armadillo.

In the dog (Evans 1993: 149), the nasal bone's "external surface usually presents a small foramen at its midlength for the transmission of a vein." In the yellow armadillo, between two and four small foramina are present (Fig. 1). In the remaining xenarthrans (*Dasyurus kappleri* CM 76828, *Bradypus variegatus* CM 4457, *Tamandua tetradactyla* CM 78750, and *T. mexicana* CM 21007), there are two to three tiny foramina per side, asymmetrically arranged. *Metacheiromys* sp. YPM-PU 18107 has a number of very small, asymmetrically

arranged foramina clustered close to the midline and near the suture between the maxilla and the nasal. None is reported for *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004).

Occipital Groove.—In humans (Clemente 1985), the occipital artery runs posteriorly across the right and left temporal bones in a shallow sulcus, the occipital groove, medial to the mastoid process and the mastoid notch, which houses the posterior digastric muscle. In the dog (Evans 1993), the course of the occipital artery on the mastoid is not indicated. In the yellow armadillo (Fig. 5), the occipital groove for the occipital artery and vein is very deep, near vertical, and runs nearly the extent of the mastoid exposure of the petrosal bone, from dorsal to the stylohyal fossa to the supraoccipital bone; in CM 6398, 61426, and 101007, the occipital groove extends onto the supraoccipital bone. Within the occipital groove near the supraoccipital suture are the two posterior openings into the posttemporal canal. On the right side of CM 6399 and 101007, near the midpoint of the occipital groove is a narrow bridge of bone that encircles the groove to form a very short canal.

In *Dasyurus kappleri* CM 76828, the occipital groove is deep, runs the length of the mastoid exposure of the petrosal, and extends dorsally onto the squamosal; it contains two posterior openings into the posttemporal canal. The occipital groove is absent in *Bradypus variegatus* CM 4457, *Tamandua tetradactyla* CM 78750, *T. mexicana* CM 21007, *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* (Wible et al. 2004). However, the occipital groove is known to occur in other *Bradypus* (Gaudin 1995). A shallow occipital groove is also present in both *Metacheiromys* and *Palaeamodon*. In the former (YPM-PU 18107), it travels across the mastoid just posterior to the nuchal crest. In the latter (Patterson et al. 1992), it begins close to the jugular/paracondylar process ventrally, well posterior to the nuchal crest, but converges on the nuchal crest dorsally as it traverses the occipital surface of the mastoid, entering the posterior opening of the posttemporal canal at roughly the level of the dorsal rim of the foramen magnum.

Gaudin (1995) used two five-state characters pertaining to the occipital groove: character 59, connection of the stylomastoid foramen and foramina for the occipital artery/arteria diploëtica magna, and character 69, grooves, canals and foramina of the occipital artery and the arteria diploëtica magna. Gaudin and Wible (in press: character 162) used the continuation of the occipital groove dorsal to posterior opening of the posttemporal canal as a character.

Optic Canal.—In the dog (Evans 1993), the optic canal is visible in lateral view, situated in the center of the right and left orbital wings of the presphenoid bone (orbitosphenoid), and transmits the optic nerve, the

internal ophthalmic artery off the Circle of Willis (=ophthalmic artery of this report), and the internal ophthalmic vein. In the yellow armadillo (Fig. 3B), the optic canal is visible in lateral view, dorsocentrally located in the orbitosphenoid, and transmits the same structures as in the dog. Most specimens studied have a ridge running forward from the ventral aspect of the optic canal that represents the ossified ala hypochiasmatica for the attachment of extraocular muscles.

In *Dasyurus kappleri* CM 76828, the optic canal is centrally located in the orbitosphenoid, but hidden within the sphenorbital fossa and not visible in lateral view. The ossified ala hypochiasmatica is a raised ridge that ends in a point anteriorly. In *Bradypus variegatus* CM 2180 and 4457, the optic canal is posteroventrally located in the orbitosphenoid and hidden within the sphenorbital fossa. Visible in lateral view is a deep groove that runs anteriorly and slightly dorsally from the optic canal; the raised ventral edge of this groove is the ossified ala hypochiasmatica. In the *Tamandua* (*T. tetradactyla* CM 6340 and 78750 and *T. mexicana* CM 21007), the optic canal is partially hidden in lateral view, is positioned between the orbitosphenoid and the palatine, and the left and right sides are confluent. There is no raised ridge representing the ossified ala hypochiasmatica. In *Metacheiromys* (YPM-PU 18107; Simpson 1931), *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* (Wible et al. 2004), the optic canal is visible in lateral view and centrally located within the orbitosphenoid.

MacPhee (1994: character 1) used the size of the optic canal relative to the infraorbital foramen as a character. Gaudin (2004: character 160) examined the position of the optic canal relative to the sphenorbital fissure (separate or opening externally into a common aperture). Gaudin and Wible (in press: characters 79 and 80) used two characters of the optic canal: whether it is visible in lateral view and its position within the orbitosphenoid.

Orbitotemporal Canal, Anterior Opening.—In various extant placentals, the anterior division of the stapedial artery (and accompanying vein) enters the orbit as the ramus supraorbitalis (Wible 1987) via an aperture that is called variously the sinus canal (Gregory 1910; McDowell 1958), the cranio-orbital foramen (Saban 1956/1957; MacPhee 1994), and the anterior opening of the orbitotemporal canal (Rougier et al. 1992; Wible et al. 2004). We prefer the last term, because it best describes the position of this vascular canal and its orbital egress, and it best reflects the broader homology of these structures because it has already been applied to a broad spectrum of cynodonts (see Rougier et al. 1992).

The orbitotemporal canal and its anterior opening are lacking in the dog (Evans 1993). In the yellow armadillo (Fig. 3B), the anterior opening is entirely within the frontal, posterodorsal to the dorsal ethmoidal

foramen, and transmits the ramus supraorbitalis and companion vein.

In *Dasyurus kappleri* CM 76828, the anterior opening of the orbitotemporal canal is in the frontal on the right, but the floor has a small contribution from the orbitosphenoid on the left. The anterior opening is absent in *Bradypus variegatus* CM 2180 and 4457, *Tamandua tetradactyla* CM 9340 and 78750, and *T. mexicana* CM 21007. The anterior opening is within the frontal in *Leptictis dakotensis* (labeled as ethmoidal foramen in Novacek 1986: fig. 10) and between the frontal, orbitosphenoid, and alisphenoid in *Zalambdalestes lechei* (Wible et al. 2004). The condition in *Metacheiromys* is unknown.

Gaudin and Wible (in press: character 78) used the presence/absence of the anterior opening of the orbitotemporal canal as a character.

Parietal Foramina.—In humans, parietal foramina are small openings just off the midline in the paired parietals transmitting emissary veins; they are variably present and differ in number, position, and symmetry (Boyd 1930). Parietal foramina are not described for the dog, but one with an emissary vein is figured (Evans 1993: fig. 12-22). In the yellow armadillo, there are approximately 10 tiny apertures per side, asymmetrically arranged, in FMNH 28350 (Figs. 1A, 2A).

In *Dasyurus kappleri* CM 76828, there are roughly a half dozen tiny foramina per side, asymmetrically arranged. In *Bradypus variegatus* CM 4457, there is one small foramen on the left side only, near the supraoccipital. In *Tamandua tetradactyla* CM 78750, there is one tiny foramen per side just anterior to the supraoccipital, symmetrically placed, and two more rostral tiny foramina on the right side only. In *T. mexicana* CM 21007, there is one tiny foramen per side, symmetrically placed, just anterior to the supraoccipital, and an additional one per side that is more posterolateral on the right and anterolateral on the left. Parietal foramina are not reported or figured for *Metacheiromys* (Simpson 1931), *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* (Wible et al. 2004).

Piriform Fenestra.—Following MacPhee (1981), the piriform fenestra is the large gap seen in all fetal mammals and in a few adults anterior to the auditory capsule, usually between that element, the sphenoid (basisphenoid and alisphenoid), and the squamosal. These bones are in close contact in the adult dog (Evans 1993), and, therefore, the piriform fenestra is absent. In the yellow armadillo, CM 61426, a narrow piriform fenestra is visible between the petrosal, basisphenoid, and alisphenoid, lateral to and continuous with the carotid foramen.

In *Dasyurus kappleri* CM 76828, a sizeable piriform fenestra, continuous with the carotid foramen, basisphenoid fissure, and jugular foramen, is present in front

of the entire anterior aspect of the petrosal; it is bordered anteriorly by the alisphenoid and the squamosal. The piriform fenestra is lacking in *Bradypus variegatus* CM 2180 and *Tamandua tetradactyla* CM 91944. The condition is unknown in *Metacheiromys*, but a patent piriform fenestra is clearly absent in *Palaeonodon* (Patterson et al. 1992). It is also lacking in *Leptictis dakotensis* (Novacek 1986), but is present in *Zalambdalestes lechei*, between the basisphenoid, alisphenoid, and petrosal, separated from the carotid foramen (Wible et al. 2004).

Gaudin and Wible (in press: character 109) used the presence/absence of the piriform fenestra as a character.

Postglenoid Foramen.—In the dog (Evans 1993), the retroarticular foramen (=postglenoid foramen) lies in the right and left squamosals, behind the retroarticular process (=postglenoid process), and transmits the retroarticular vein (=capsuloparietal emissary vein). In the yellow armadillo (Figs. 4A, B), the postglenoid foramen for the capsuloparietal emissary vein lies within the squamosal in a depression behind the glenoid fossa, dorsal to the front edge of the external acoustic porus and anterior to the postglenoid process. One foramen occurs bilaterally except for the left side of FMNH 28350 and CM 10743 in which it is trifurcated.

In *Dasybus kappleri* CM 76828, the postglenoid foramen is posterodorsal to the glenoid fossa and medial to the feeble postglenoid process. In living pilosans, well-developed postglenoid foramina are lacking (Gaudin 1995). In *Bradypus variegatus*, a tiny postglenoid foramen is situated medial to the weak postglenoid process in the juvenile, CM 2180, but appears to be lacking in the adult, CM 4457. In *Tamandua tetradactyla* CM 78750, two tiny foramina are situated anterior to the feeble postglenoid process (visible in the juvenile CM 6340) that may represent postglenoid foramina; these are lacking in *T. mexicana* CM 21007. *Metacheiromys* lacks a postglenoid foramen (YPM-PU 18107; Simpson 1931), but a large postglenoid foramen is present in *Palaeonodon* (Patterson et al. 1992) posteromedial to the large postglenoid process. In *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004), the postglenoid foramen is posterior and anterior to the sizeable postglenoid process, respectively.

As noted in the descriptions, Patterson et al. (1989) reported that the postglenoid process is lacking in xenarthrans with the exception of the Eocene armadillo *Utaetus buccatus*. Juvenile xenarthrans examined here contradict this observation. The juvenile yellow armadillo CM 10743 has a tall postglenoid process that extends to the ventral margin of the external acoustic porus. The juvenile three-toed sloth CM 2180 has a short, but distinct postglenoid process that apparently is fused to the anterior crus of the ectotympanic in the adult CM 4457, and the juvenile tamandua CM 6340 has a feeble postglenoid

process that is nearly fused with the anterior crus of the ectotympanic.

Gaudin (1995: character 84) coded the postglenoid foramen as either reduced/absent or present. Gaudin and Wible (in press: character 119) used the presence of a distinct depression for the postglenoid foramen behind the glenoid fossa, as occurs in the yellow armadillo, as a character.

Posttemporal Canal, Posterior Opening.—In monotremes and some placentals, the posterior division of the stapedia artery, the arteria diploëtica magna of Hyrtl (1853, 1854), and accompanying vein run in a canal between the petrosal and the squamosal that opens onto the occiput (Wible 1987; Wible and Hopson 1995). The term generally used for this paired canal in the literature of non-mammalian cynodonts is posttemporal canal, which following Wible (1989) and Rougier et al. (1992), we employ here.

The posttemporal canal is absent in the dog (Evans 1993). The yellow armadillo has two posterior openings into the posttemporal canal, one situated above the other, near the dorsal limit of the mastoid exposure of the petrosal (Fig. 5). Both foramina are within the petrosal in FMNH 28350, but in the remaining specimens, the slightly smaller superior foramen has a small contribution from the supraoccipital. Based on the fetal yellow armadillo, the inferior foramen transmits the arteria diploëtica magna from the occipital artery and the superior foramen the vena diploëtica magna.

Dasybus kappleri CM 76828 also has two posterior openings into the posttemporal canal within the mastoid exposure of the petrosal, but the inferior one is more than twice the size of the superior one. A weak arteria diploëtica magna is reported for adult *Bradypus torquatus* (Hyrtl 1850) and *Choloepus hoffmanni* (Bugge 1979) and for fetal *Bradypus* sp. (Wible 1984), but a posterior opening of the posttemporal canal is wholly absent in *Bradypus variegatus* CM 2180 and 4457. A well-developed arteria diploëtica magna is reported for fetal and adult *Tamandua tetradactyla* (Hyrtl 1854; Bugge 1979; Wible 1984), but its point of entry differs from that of the armadillos; its aperture is between the parietal and squamosal. In *T. tetradactyla* CM 6340 and *T. mexicana* CM 21007, one large foramen in the parietal-squamosal suture (within the squamosal on the right side of the latter), dorsal to the external acoustic meatus, opens into the posttemporal canal, which runs both anteriorly and posteriorly from the external aperture. In contrast, in *T. tetradactyla* CM 78750, there are three foramina on the left side and four on the right in the comparable location. The posterior opening of the posttemporal canal is between the squamosal and the mastoid exposure of the petrosal in *Metacheiromys* sp. YPM-PU 18107 and USNM 452349 and *Zalambdalestes lechei* (Wible et al. 2004), but is absent in *Leptictis dakotensis* (Novacek 1986).

MacPhee (1994: character 13) used the presence/absence of the posterior opening as a character. Gaudin (1995) used two five-state characters pertaining to the posterior opening of the posttemporal canal: character 59, connection of the stylomastoid foramen and foramina for the occipital artery/arteria diploëtica magna, and character 69, grooves, canals and foramina of the occipital artery and arteria diploëtica magna. Gaudin and Wible (in press: character 161) used the squamosal participation in the lateral wall of the posterior opening of the posttemporal canal as a character.

Pterygoid Canal.—In the dog (Evans 1993), an extremely small pterygoid groove on the right and left sides of the basisphenoid runs anteriorly into a minute pterygoid canal. The caudal opening of the pterygoid canal is in the suture between the basisphenoid and the pterygoid, and the rostral opening is in the caudal part of the pterygopalatine fossa, between the pterygoid and the pterygoid process of the sphenoid (the ventral projection of the sphenoid that abuts the pterygoid bone). Transmitted are the nerves of the pterygoid canal and occasionally a small artery of the pterygoid canal off the maxillary artery. As in the dog, the yellow armadillo has a pterygoid groove posteriorly in the basipharyngeal canal and a pterygoid canal anteriorly that extends into the back of the orbit. The pterygoid groove is on the medial side of the pterygoid and/or alisphenoid, and its posterior part may be enclosed in a short canal in the pterygoid (Fig. 4C). The pterygoid canal has a caudal opening in the basipharyngeal canal either within the pterygoid, between the pterygoid and palatine, or between the alisphenoid and palatine, and a rostral opening visible in lateral view is in the back of the orbit below the sphenorbital fissure, between the orbitosphenoid, palatine, and alisphenoid (Fig. 3B). Transmitted are the nerves of the pterygoid canal, accompanying vein, and a small branch of the maxillary artery.

In *Dasypus kappleri* CM 78628, the pterygoid groove of the yellow armadillo is fully enclosed in bone, resulting in an elongate pterygoid canal with a caudal opening immediately in front of the ear region, within the basisphenoid on the right and between the basisphenoid and the pterygoid on the left. The rostral opening is not visible in lateral view, but is in the anteriormost floor of the sphenorbital recess, between the orbito- and alisphenoid. In *Bradypus variegatus* CM 4457, a shallow pterygoid groove on the alisphenoid leads into the caudal opening of the pterygoid canal within the palatine; the rostral opening is visible in lateral view below the sphenorbital fissure within the palatine. The juvenile *B. variegatus* CM 2180 differs in that the pterygoid groove is in the pterygoid and the caudal opening is within the pterygoid, near the palatine suture. In *Tamandua tetradactyla* CM 6340, the shallow pterygoid groove on the basisphenoid leads to the caudal opening between the

pterygoid and the palatine; the rostral opening based on CM 78750 is visible in lateral view, anteroventral to the sphenorbital fissure, within the palatine. No rostral opening is reported or figured for *Leptictis dakotensis*; the caudal opening appears to be within the alisphenoid (Novacek 1986: figs. 22, 23). The course of the nerves of the pterygoid canal is unknown in *Metacheiromys* and *Zalambdalestes lechei*.

Gaudin and Wible (in press: characters 82, 106, and 107) used characters for the positions of the rostral and caudal openings of the pterygoid canal: for the former, its relationships to the sphenorbital fissure and for the latter, its position and bone(s) of enclosure.

Sphenopalatine Foramen.—In the dog (Evans 1993), the sphenopalatine foramen for the caudal nasal nerve and sphenopalatine artery is within the perpendicular lamina of the right and left palatines anterodorsal to and separated by a narrow septum from the caudal palatine foramen. In the yellow armadillo (Fig. 3B), the comparable foramen lies between the maxilla and palatine and is confluent with the larger more posteroventrally placed caudal palatine foramen, although some separation of the two foramina occurs in FMNH 28350 and CM 61426.

In *Dasypus kappleri* CM 76828, the sphenopalatine and caudal palatine foramina are confluent, located between the palatine, pterygoid, and ethmoid on the right side and between the pterygoid and ethmoid on the left. There is a distinct longitudinal sulcus extending the length of the orbital exposure of the ethmoid, from the front of the sphenorbital fissure, that runs into the confluent sphenopalatine/caudal palatine foramina from behind. In *Bradypus variegatus* CM 4457, the sphenopalatine and caudal palatine foramina are separated from each other; both are in the palatine but the latter is centrally placed and the former is anterodorsal. There is a short, broad, shallow sulcus in the palatine that runs into the sphenopalatine foramen from above and behind. In *Tamandua tetradactyla* CM 78750, the sphenopalatine and caudal palatine foramina occupy a common depression in the palatine, but are separated by a stout septum; the sphenopalatine foramen is anterior to the caudal palatine foramen. In *Metacheiromys* sp. YPM-PU 18107, there is a large foramen between the palatine and the frontal that almost certainly housed the openings for the sphenopalatine and caudal palatine foramina, but it is not known whether these openings were separate or confluent. In *Leptictis dakotensis* (Novacek 1986, but see Asher 1999) and *Zalambdalestes lechei* (Wible et al. 2004), the sphenopalatine and caudal palatine foramina are confluent, between the palatine and the orbitosphenoid in the former and between the palatine, frontal, and maxilla in the latter. In *Z. lechei*, a distinct groove in the maxilla connects the sphenopalatine and maxillary foramina.

Gaudin (2004: character 161) used the position of the sphenopalatine foramen relative to the sphenorbital fissure/optic foramen as a character. Gaudin and Wible (in press: character 71 and 73) used the number of sphenopalatine/caudal palatine foramina and the presence/absence of a groove connecting the sphenopalatine/caudal palatine foramina and the sphenorbital fissure as characters.

Sphenorbital Fissure.—In the dog (Evans 1993), the orbital fissure (=sphenorbital fissure) lies lateral to the body of the sphenoid in the suture between the right and left orbito- and alisphenoids. It transmits the oculomotor, trochlear, ophthalmic, and abducens nerves, the anastomotic artery connecting the maxillary and internal carotid arteries, and the ophthalmic venous plexus. In the yellow armadillo (Fig. 3B), the sphenorbital fissure is between the orbitosphenoid medially and the alisphenoid laterally and transmits the oculomotor, trochlear, ophthalmic, maxillary, and abducens nerves, accompanying veins, and a tiny branch of the maxillary artery.

In the remaining taxa examined here, the sphenorbital fissure lies between the orbito- and alisphenoid with one exception: in *Bradypus variegatus* CM 4457, there is a small contribution to the lateral wall from the squamosal.

Stapedial Artery Groove.—The stapedial artery arises on each side from the internal carotid artery in the platypus and in various extant plaeentals (Tandler 1899, 1901; Bugge 1974; Wible 1987). Among the latter, the artery often runs on the back of the promontorium of the petrosal in a groove directed at the fenestra vestibuli (Wible 1987). The promontorial stapedial groove and the promontorial part of the stapedial artery are lacking in the dog (Evans 1993) and in the fetal and adult yellow armadillos studied here (Fig. 4) and by Tandler (1901).

A stapedial artery is lacking in the remaining adult xenarthrans dissected to date: *Dasypus novemcinctus* (Tandler 1899; Bugge 1979), *Chaetophractus villosus* (= *Dasypus villosus*, Tandler 1899), *Chlamyphorus truncatus* (= *Chlamydophorus truncatus*, Tandler 1899), *Bradypus torquatus* (Tandler 1899), *Choloepus hoffmanni* (Bugge 1979), and *Tamandua tetradactyla* (= *Myrmecophaga tamandua*, Tandler 1899; Bugge 1979). A groove for the stapedial artery is absent in *Dasypus kappleri* CM 76828, *Bradypus variegatus* CM 4457, and *Tamandua mexicana* CM 21007. A stapedial groove is also absent in *Metacheiromys* (Patterson et al. 1992). In contrast, a promontorial groove for the stapedial artery is present in the Paleocene *Palaeonodon* (Patterson et al. 1992), *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* (Wible et al. 2004).

Stylomastoid Foramen.—In the dog (Evans 1993), the stylomastoid foramen is the opening that transmits the

facial nerve from the middle ear to the posterolateral surface of the auditory bulla. It is in the posterolateral aspect of the auditory bulla entirely within the right and left petrous temporal bones and also is occupied by the stylomastoid artery (sometimes double) off the caudal auricular artery. In the yellow armadillo, the foramen that transmits the facial nerve from the middle ear is not visible on the skull base, but is enclosed in the posteromedial part of the external acoustic meatus. In the fetus, in addition to the facial nerve, this opening transmits the stylomastoid artery off the occipital artery. The opening that transmits the facial nerve from the external acoustic meatus to the skull base is the foramen stylomastoideum tertium (see above) between the ectotympanic and paroccipital process of the petrosal.

In the remaining taxa examined, the stylomastoid foramen connects the middle ear and the skull base. In *Dasypus kappleri* CM 76828 and *Bradypus variegatus* CM 2180, the stylomastoid foramen is between the tympanohyal ventrally and the petrosal dorsally, with the posterior crus of the ectotympanic underlying the tympanohyal, which is ossified with the petrosal. In *Tamandua tetradactyla* CM 6340, the foramen is between the posterior crus of the ectotympanic ventrally and another element dorsally; the latter is the squamosal based on Guth (1961: fig. 17). In *Metacheiromys* (YPM-PU 18107; Simpson 1931), the stylomastoid foramen lies between the paroccipital process of the petrosal and the tympanohyal, with perhaps some participation by the posterior crus of the ectotympanic in its anterior margin. Rather than a closed foramen, *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004) have a stylomastoid notch open medially formed at the tympanohyal's attachment to (and fusion with) the crista parotica.

Gaudin (1995: characters 57 and 58) used the position of the stylomastoid foramen relative to the tympanohyal/stylohyal fossa and the direction of the stylomastoid foramen as characters.

Subsquamosal Foramina.—See foramina for rami temporales above.

Sulcus for Greater Petrosal Nerve.—See hiatus Fallopii above.

Sulcus for Mylohyoid Nerve.—A sulcus for the mylohyoid nerve on the mandibular ramus below the mandibular foramen is not reported for the dog (Evans 1993). The yellow armadillo has a weak sulcus that begins posterior to the ventral edge of the mandibular foramen, runs ventrally and slightly anteriorly, and fades out as it approaches the ventral margin of the mandibular ramus (Fig. 7B).

A weak sulcus resembling that in the yellow armadillo is present on the right side of *Dasypus kappleri*

CM 76828, but is entirely lacking on the left side. *Bradypus variegatus* CM 4457 has a weak sulcus for the mylohyoid nerve that is well posterior to the mandibular foramen; its dorsal end is halfway between the mandibular foramen and the posterior border of the mandibular ramus. A mylohyoid sulcus is absent in *Tamandua tetradactyla* CM 78750 and *T. mexicana* CM 21007 and apparently also in the Cretaceous leptictid *Gypsonictops hypoconus* (Clemens 1973) and *Zalambdalestes lechei* (Kielan-Jaworowska and Trofimov 1981). The sulcus is clearly present, however, in both *Metacheiromys dasypus* (Simpson 1931) and *Metacheiromys* sp. YPM-PU 18107, extending ventrally and slightly anteriorly from the posteroventral margin of the mandibular foramen as in the yellow armadillo.

Suprameatal Foramen.—Following Novacek (1986), Wible (2003), and Wible et al. (2004), we identify the foramen in the left and right squamosals dorsal to the external acoustic porus and ventral to the suprameatal bridge as the suprameatal foramen. In the yellow armadillo, the suprameatal foramen is situated dorsal to posttympanic process of the squamosal, is single, except on the left side of FMNH 28350 (Fig. 3A) in which a thin septum divides the external orifice, and based on the fetus transmits a ramus temporalis of the stapedial system and accompanying vein.

In *Dasypus kappleri* CM 76828, the suprameatal foramen is also dorsal to the posttympanic process and is entirely within the squamosal on the left side as in the yellow armadillo, but between the squamosal and parietal on the right. The foramen is lacking in *Bradypus variegatus* CM 4457, *Tamandua tetradactyla* 78750, *T. mexicana* CM 21007, and *Metacheiromys*, as well as in the dog (Evans 1993). In *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004), the suprameatal foramen is within the squamosal, anterior to the level of the posttympanic process.

Gaudin and Wible (in press: character 120) used the number of suprameatal foramina as a character.

Supraoccipital Foramina.—In the dog (Evans 1993: figs. 12–21, 12–22), a foramen in the squamous part of the occipital bone (supraoccipital) transmitting a venous connection between the transverse sinus and the occipital emissary vein is illustrated, but not described in the text. In the yellow armadillo (Fig. 5), the number, size, and position of (nutrient?) foramina in the supraoccipital bone varies from none in CM 10743 to a dozen on the right side of CM 61426.

Only three forms examined here have small foramina in the supraoccipital. *Dasypus kappleri* CM 76828 has a small foramen centrally positioned to the right of the external occipital crest, Simpson (1931: 22) noted that “the supraoccipital [of *Metacheiromys dasypus*] is irregularly pierced by several foramina,” and *Zalambdalestes*

lechei has numerous small openings below the nuchal crest (Kielan-Jaworowska 1984).

Transverse Canal Foramen.—Most extant marsupials have a transverse canal foramen in the right and left sides of the basisphenoid that transmits a vein from the cavernous sinus and that in some forms communicates across the midline with its antimeres (Sánchez-Villagra and Wible 2002). This foramen is absent in the dog (Evans 1993), *Bradypus variegatus* CM 4457, *Tamandua tetradactyla* CM 78750, *T. mexicana* CM 21007, *Metacheiromys* (YPM-PU 18107; Simpson 1931), *Leptictis dakotensis* (Novacek 1986), and *Zalambdalestes lechei* (Wible et al. 2004). In contrast, a transverse canal foramen is present in the alisphenoid of the yellow armadillo; it sits in a depression anteroventral to the foramen ovale (Fig. 3B). The same arrangement is present in *Dasypus kappleri* CM 76828 and is figured for *D. novemcinctus* by MacPhee (1994: fig. 8). In the fetal yellow armadillo, this aperture accommodates a large distributary of the cavernous sinus.

Gaudin and Wible (in press: character 111) used the presence/absence of the transverse canal foramen as a character.

Ventral Condylloid Foramen.—In the yellow armadillo, there are two or three small, presumably nutrient foramina posterolateral to the hypoglossal foramen and anterodorsal to the anterior edge of each occipital condyle that we identify as ventral condylloid foramina in light of their occurrence in the ventral condylloid fossa (not visible in the figures). *Dasypus kappleri* CM 76828 has two such tiny foramina and *Bradypus variegatus* CM 4457 one small foramen on the left side only. *Tamandua tetradactyla* CM 78750 lacks ventral condylloid foramina, but *T. mexicana* CM 21007 has two small foramina on the left and one on the right. Such foramina are not reported for *Leptictis dakotensis* (Novacek 1986) and *Zalambdalestes lechei* (Wible et al. 2004). The condition in *Metacheiromys* is unknown.

The dog does not have ventral condylloid foramina, but does have a condylloid canal that runs through the endocranial surface of the right and left lateral parts of the occipital (exoccipital bones), has an intraosseous connection with the hypoglossal canal and usually with the petrobasilar fissure, and transmits a well-developed condylloid vein (Evans 1993).

DISCUSSIONS AND CONCLUSIONS

Comparisons of the cranial osteology of the examined sample of *Euphractus sexcinctus* with that of other taxa for the purposes of phylogenetic analysis, as models for interpreting extinct forms, and for standardization of terminology are among the ultimate goals of this study. Three sorts of limited comparisons are presented (limited

because of the small size of the samples studied): within the individual *E. sexcinctus*, between the six examined crania of *E. sexcinctus*, and with seven selected outgroups (the dasypodid *Dasypus kappleri*, the bradypodid *Bradypus variegatus*, the myrmecophagids *Tamandua tetradactyla* and *T. mexicana*, the Eocene palaeonodont *Metacheiromys*, the Oligocene placental *Leptictis*, and the Late Cretaceous eutherian *Zalambdalestes*).

Individual Variation

Some features exhibit left/right asymmetry in the studied sample of yellow armadillos. We summarize these features here in descending order, beginning with those exhibiting asymmetry in the entire sample.

Major, Accessory, and Minor Palatine Foramina.—The numerous foramina in the palatal process of the maxilla and the horizontal process of the palatine identified here as major, accessory, and minor palatine foramina (Figs. 1B, 2B) exhibit left-right asymmetry in position, size, and number in each of the six yellow armadillos (Fig. 9).

Foramina for Rami Temporales.—The numerous foramina in the parietal and squamosal as well as in the sutures between these bones and the frontal that transmit rami temporales of the stapedial artery (Figs. 1A, C, 2A, C, 3A) exhibit left/right asymmetry in position, size, and number in each of the six yellow armadillos (Fig. 8).

Foramina in Frontal, Dorsal, and Temporal Surfaces.—The numerous foramina in the frontal that transmit branches of the external ethmoidal artery or rami temporales of the stapedial artery (Figs. 1A, C, 2A, C, 3A) exhibit left/right asymmetry in position and size in each of the six yellow armadillos (Fig. 8). The specimens also vary in number except in CM 10743, which has the same on the left and right sides dorsally, and CM 61426, which has the same on the left and right sides temporally.

Supraoccipital Foramina.—The nutrient foramina in the supraoccipital (Fig. 6) exhibit left/right asymmetry in position, size, and number in each of the five yellow armadillos with such foramina; the juvenile CM 10743 lacks supraoccipital foramina.

Dorsal Condylloid Foramen.—Foramina in the dorsal condylloid fossa exhibit left/right asymmetry in position, size, and number in four of the five yellow armadillos with such foramina (FMNH 28350, CM 6398, 6399, and 101007); foramina are absent in CM 10743.

Nerves of the Pterygoid Canal.—The course of the nerves of the pterygoid canal along the walls of the basipharyngeal canal (Fig. 4) exhibit left/right asymmetry

in the form of an open sulcus on one side and with some closure on the other in three of the six yellow armadillos (FMNH 28350, CM 61426 and 101007).

Mental Foramen.—The number of mental foramina (Fig. 7A) exhibits left/right asymmetry in three of five yellow armadillos (CM 6398, 6399, and 101007); CM 61426 preserves only the right mandible.

Hypoglossal Foramen.—In FMNH 28350 and CM 10743, the hypoglossal foramen (Figs. 4A, B) is single on one side and double on the other; it is single elsewhere except in CM 61426 in which it is double bilaterally.

Occipital Groove.—In CM 6399 and 101007, the middle part of the right occipital groove (Fig. 6) is enclosed by a narrow bridge to form a closed canal; it is open elsewhere.

Nasal Foramina.—The number of nasal foramina (Figs. 1A, 2A) exhibits left/right asymmetry in FMNH 28350 and CM 6398, but not elsewhere.

Postglenoid Foramen.—In FMNH 28350 and CM 10743, the postglenoid foramen (Figs. 4A, B) is single on one side and trifurcated on the other; it is single elsewhere.

Suprameatal Foramen.—In CM 6399, the suprameatal foramen is present on the right side only, and in FMNH 28350, the suprameatal foramen is single on the right and bifurcated on the left (Fig. 3A); it is single elsewhere.

Caudal Palatine and Sphenopalatine Foramina.—These two foramina (Fig. 3B) are fully separated on the right side of FMNH 28350, but confluent elsewhere.

Lacrimal Foramen.—This foramen (Fig. 3A) is divided by a septum on the right side of FMNH 28350, but not elsewhere.

Ala Hypochiasmatica.—This short ridge ventral and anterior to the optic canal (Fig. 3A) is wholly lacking from the right side of FMNH 28350, but not elsewhere.

Carotid Canal.—A carotid canal occurs in three of the six yellow armadillos, CM 6399, 61426, and 101007 (Figs. 9C, E, F); in CM 61426 it is not entirely closed on the left side.

Sulcus between Inferior Petrosal Sinus Foramen and Hypoglossal Foramen.—A distinct venous sulcus (Figs. 4A, B) connects the inferior petrosal sinus foramen and the hypoglossal foramen in four of the six yellow

armadillos (FMNH 28350, 6398, 6399, and 101007); in the last it occurs only on the left side (Figs. 9A–C, F).

Intraspecific Comparisons

Five subspecies of *Euphractus sexcinctus* are generally recognized (Yepes 1928; Cabrera 1958; Wetzel 1982; Redford and Wetzel 1985). Five of the specimens studied by us (FMNH 28350 and CM 6398, 6399, 10743, and 61426) are from the Gran Chaco of Santa Cruz, southeastern Bolivia and western Mato Grosso, Brazil, and the sixth (CM 101007) is from the caatinga of Pernambuco, northeastern Brazil. The former specimens are in the range of *E. s. bolivae* and the latter in the range of *E. s. setosus*.

Few differences in cranial morphology have been identified among these subspecies. Yepes (1928) noted differences in the nasal bones between *Euphractus sexcinctus bolivae* and *E. s. tucumanus*; in the former, the lateral borders of the nasal are parallel, whereas in the latter they are wide at the level of the premaxillary-maxillary suture. Unfortunately, in the sample studied by us, the nasals of the forms from the range of *E. s. bolivae* do not conform to those described by Yepes (1928), but resemble his description of *E. s. tucumanus* (Figs. 8A–C, E).

There are numerous differences within the small sample studied by us. However, CM 101007 (*E. s. setosus*) differs from the remaining adult specimens (*E. s. bolivae*) in three features: the shape of the temporal lines, the shape of the nasals, and the shape of the back of the palate. In CM 101007, the temporal lines are situated near the orbital margin of the frontal and converge at the back of the parietal (Fig. 8F); in contrast, in the remaining adults, the temporal lines converge anterior to the frontoparietal suture and then even diverge at the back of the parietal (Figs. 2A, 8A–C, E). In CM 101007, the lateral borders of the nasals are straight, but diverge slightly posteriad (Fig. 8F); in contrast, in the remaining adults, the lateral borders are widest in the middle (Figs. 8A–C, E). In CM 101007, the palatine bones at the back of the palate form a narrow *V* (Fig. 9F), whereas in the remaining adults they are *U*-shaped (Figs. 2B, 9A–C, E). CM 101007 is a female and smaller than the remaining adults (Table 1), which are of unknown gender, but it also has sutures closed (e.g., presphenoid-basisphenoid-basioccipital) that are open in FMNH 28350. With such a paltry sample, we cannot exclude that these few differences result from gender and/or size and are not subspecific in nature. It is worth noting that the weak temporal lines, the shape of the nasals, and the back of the palate of the juvenile CM 10743 (Figs. 8D, 9D) are more similar to those of CM 101007 (Figs. 8F, 9F) than to the other adults.

Outgroup Comparisons

Following the phylogenetic studies of Delsue et al. (2002, 2003) and Gaudin and Wible (in press), structures present in *Euphractus* and *Dasylops* might be present in dasypodids (armadillos) and cingulatan (armored xenarthrans) primitively; structures present in *Bradypus* and *Tamandua* might be present in pilosans (hairy xenarthrans) primitively; and structures present in all four taxa might be present in xenarthrans primitively. Following Patterson et al. (1992), Gaudin (1995, 2004), and Szalay and Sehrenk (1998) with the palaeontodont *Metacheiromys* as the first outgroup to Xenarthra, structures present in *Metacheiromys* and Xenarthra might be present primitively in this unnamed clade.

Euphractus sexcinctus.—Distinguishing *Euphractus sexcinctus* from the outgroups examined are: (1) an endocranial cochlear canaliculus; (2) a craniopharyngeal canal; (3) a canal enclosing the posterior tympanic course of the facial nerve; (4) a foramen stylomastoideum tertium; (5) an inferior petrosal sinus foramen; (6) foramina in the temporal surface of the frontal; (7) an infraorbital canal entirely in the maxilla; (8) a lacrimal fenestra; (9) a lacrimal foramen posterior to the orbital margin; (10) longitudinal mandibular sulci; and (11) a postglenoid foramen in a depression behind the glenoid fossa and anterior to the postglenoid process.

Dasypodidae.—Distinguishing *Euphractus sexcinctus* and *Dasylops kappleri* from the outgroups are: (1) a canal or foramen for the auricular ramus of the vagus nerve; (2) an extrabullar internal carotid artery (also in *Bradypus variegatus*); (3) a carotid foramen between the basisphenoid and the petrosal (also in *Bradypus variegatus*); (4) a cavity supraochleare that is open ventrally; (5) two ethmoidal foramina; (6) a transverse canal foramen present and in a common depression with the foramen ovale; (7) no foramen rotundum; (8) foramina in the dorsal surface of the frontal; (9) a Glaserian fissure adjacent to the foramen ovale; (10) the hypoglossal foramen ventral to the jugular foramen; (11) an incisive foramen within (or nearly within) the premaxilla; (12) at least two mental foramina; (13) a piriform fenestra confluent with the carotid foramen; (14) double posterior openings of the posttemporal canal, the lower entirely within the petrosal; (15) the sphenopalatine and caudal palatine foramina confluent; and (16) more than five foramina for the rami temporales in and between the squamosal and the parietal per side.

Pilosae.—Distinguishing *Bradypus variegatus*, *Tamandua tetradactyla*, and *T. mexicana* from the outgroups are: (1) one ethmoidal foramen; (2) a foramen rotundum; (3) a Glaserian fissure separated from the foramen ovale; (4) a hypoglossal foramen level with the jugu-

lar foramen; (5) an elongate incisive foramen; (6) a maxillary foramen visible in ventral view (also in *Dasypus kappleri*); (7) one mental foramen anteriorly positioned; (8) an optic canal wholly or partially hidden in lateral view (also in *Dasypus kappleri*); (9) an optic canal positioned ventrally in the orbitosphenoid; (10) no anterior opening of the orbitotemporal canal; (11) a postglenoid foramen minute or absent; and (12) the sphenopalatine and caudal palatine foramina separate and within the palatine.

Bradypus variegatus.—Distinguishing *Bradypus variegatus* from the outgroups are: (1) an extrabullar internal carotid artery (also in Dasypodidae); (2) a carotid foramen between the basisphenoid and the petrosal (also in Dasypodidae); (3) a cavum supracochleare open dorsally; (4) a foramen ovale between the alisphenoid and the pterygoid; and (5) a posterior opening of the posttemporal canal sometimes absent.

Tamandua.—Distinguishing *T. tetradactyla* and *T. mexicana* from the outgroups are: (1) a transpromontorial internal carotid artery; (2) a carotid foramen in the basisphenoid; (3) a frontal diploic vein foramen visible in dorsal view, above the orbital rim; and (4) a posterior opening of the posttemporal canal between the squamosal and the parietal and not on occiput.

Xenarthra.—Distinguishing *Xenarthra* from the outgroups are: (1) multiple palatal foramina for the major, accessory, and minor palatine nerves and vessels; (2) no alisphenoid canal; (3) a caudal palatine foramen that includes the minor palatine nerve and vessels; (4) no inferior petrosal sinus foramen (except *Euphractus sexcinctus*); (5) a foramen for the ramus superior of the stapedia artery absent or minute; (6) the hiatus Fallopii absent (except one side of *Dasypus kappleri* and with the condition in *Tamandua* unknown); (7) a lacrimal foramen on the face (except *Euphractus sexcinctus*); (8) a mandibular foramen at the level of the alveolar plane; (9) no mastoid foramen; (10) no stapedia artery groove; (11) a closed stylomastoid foramen; (12) a rostral opening of the pterygoid canal visible in lateral view below the sphenorbital fissure (except *Dasypus kappleri*); and (13) an extrabullar internal carotid artery (except *Tamandua tetradactyla* and *T. mexicana*).

Xenarthra + *Metacheiromys*.—Distinguishing *Xenarthra* and the palaeonodont *Metacheiromys* from the outgroups are: (1) foramina for rami temporales in the parietal; (2) a musculotubal canal (except *Dasypus kappleri*) with the entotympanic forming a border; (3) an occipital groove leading to the posttemporal canal (except *Tamandua tetradactyla* and *T. mexicana*); and (4) a piriform fenestra minute or absent (except *Dasypus kappleri*).

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APPENDIX 1. *List of Anatomical Terms.*

The first term is the term used here; next to it is a reference and/or Nomina Anatomica Veterinaria (NAV) or other equivalent.

- Abducens Nerve—Nervus abducens (NAV)
 Accessory Nerve—Nervus accessorius (NAV)
 Accessory Palatine Foramen—(Wible and Rougier 2000); Middle Palatine Foramen (Novacek 1986); Minor Palatine Foramen (Evans 1993)
 Accessory Palatine Nerve—Nervus palatinus accessorius (NAV)
 Ala hypochiasmatica—(De Beer 1937; Reinbach 1952a, 1955)
 Ala orbitalis—(De Beer 1937; Reinbach 1952a, 1955)
 Ala of Vomer—Ala vomeris (NAV)
 Alicochlear Commissure—(De Beer 1937; MacPhee 1981)
 Alisphenoid—Os basisphenoidale, Ala (NAV)
 Alisphenoid Canal—(Novacek 1986); Canalis alaris (NAV)
 Angular Process—Processus angularis (NAV)
 Annular Ligament—(MacPhee 1981)
 Anterior Digastric Muscle—Musculus digastricus, Venter rostralis (NAV)
 Anterior Process of Malleus—Malleus, Processus rostralis (NAV)
 Antorbital Fossa—(Novacek 1986)
 Arteria diploetica magna—(Wible 1987)
 Ascending Pharyngeal Artery—Arteria pharyngea ascendens (NAV)
 Atrioturbinal—(Reinbach 1952a, 1952b, 1955)
 Auditory Tube—Tuba auditiva (NAV)
 Auricular Ramus of Vagus Nerve—Nervus vagus, Ramus auricularis (NAV)

 Basicochlear Fissure—(MacPhee 1981); Basiotic Fenestra (MacPhee 1994)
 Basilar Artery—Arteria basilaris (NAV)
 Basipharyngeal Canal—(Evans 1993)
 Basioccipital—Os occipitale, Pars basilaris (NAV)
 Basisphenoid—Os basisphenoidale, Corpus (NAV)
 Body of Mandible—Corpus mandibulae (NAV)
 Buccinator Muscle—Musculus buccinator (NAV)

 Caninus Muscle—Musculus caninus (NAV)
 Capsuloparietal Emissary Vein—(Gelderen 1924); Vena emissaria foraminis retroarticularis (NAV); Postglenoid Vein (Butler 1967); Petrosquamous Sinus (MacPhee 1981); External Jugular Vein (Novacek 1986)
 Carotid Foramen—(Wible 2003); Anterior Carotid Foramen (MacPhee 1981; Novacek 1986); Foramen Lacerum Medium (Patterson et al. 1989)
 Carotid Canal—Canalis caroticus (NAV)
 Carotid Sulcus—Sulcus caroticus (NAV)
 Canal for Auricular Ramus of Vagus—New term
 Caudal Nasal Nerve—Nervus nasalis caudales (NAV)
 Caudal Palatine Foramen—(Evans 1993); Postpalatine Foramen (Novacek 1986; MacPhee 1994)
 Caudal Tympanic Process of Petrosal—(MacPhee 1981)
 Cavernous Sinus—Sinus cavernosus (NAV)
 Cavum epiptericum—(Gaupp 1908; De Beer 1937)
 Cavum supracochleare—(Voit 1909; De Beer 1937)
 Cavum tympani—(NAV)
 Cerebrum—(NAV)
 Choanae—(NAV)
 Chorda Tympani Nerve—Chorda tympani (NAV)
 Cochlear Canaliculus—Canaliculus cochleae (NAV); Aquaeductus cochleae (Novacek 1986)
 Cochlear Duct—Ductus cochlearis (NAV)
 Cochlear Fossula—(MacPhee 1981)
 Condylar Process—Processus condylaris (NAV)
 Condylod Artery—Arteria condylaris (NAV)
 Coronoid Crest—(Evans 1993)

 Coronoid Process—Processus coronoideus (NAV)
 Craniopharyngeal Canal—Canalis craniopharyngeus (NAV)
 Cribriform Plate—Os ethmoidale, Lamina cribrosa (NAV)
 Crista interfenestralis—(Wible et al. 1995)
 Crista parotica—(De Beer 1937; MacPhee 1981); Crista Facialis (Patterson et al. 1989)
 Crista tympanica—(MacPhee 1981)
 Crus breve—(NAV)
 Crus longum—(NAV)

 Deep Petrosal Nerve—Nervus petrosus profundus (NAV)
 Dens of Axis—Axis, Dens (NAV)
 Dorsal Condylod Foramina—New term
 Dorsal Condylod Fossa—Fossa condylaris dorsalis (NAV)
 Dorsal Nasal Meatus—Meatus nasi dorsalis (NAV)

 Ectotympanic—Os temporale, pars tympanica (NAV)
 Entoglenoid Process of Squamosal—(McDowell 1958); Preotic Crest of Squamosal (Novacek 1986)
 Entopterygoid Crest—(Novacek 1986)
 Entotympanic—Os temporale, Pars endotympanica (NAV)
 Epitympanic Recess—Recessus epitympanicus (NAV)
 Epitympanic Sinus—(Klaauw 1931)
 Epitympanic Wing of Petrosal—(MacPhee 1981)
 Ethmoid—Os ethmoidale (NAV)
 Ethmoidal Foramen—Foramen ethmoidale (NAV)
 Ethmoidal Nerve—Nervus ethmoidale (NAV)
 Ethmoturbinal—Ethmoturbinalia (NAV)
 Exoccipital—Os occipitale, Pars lateralis (NAV)
 External Acoustic Meatus—Meatus acusticus externus (NAV)
 External Acoustic Porus—Porus acusticus externus (NAV)
 External Carotid Artery—Arteria carotis externa (NAV)
 External Ethmoidal Artery—Arteria ethmoidalis externa (NAV)
 External Nasal Aperture—Apertura nasi osseum (NAV)
 External Nasal Ramus of Ethmoidal Nerve—Nervus ethmoidalis, Ramus nasalis externi (NAV)
 External Occipital Crest—Crista occipitalis externa (NAV)

 Facial Canal—(MacPhee 1981)
 Facial Nerve—Nervus facialis (NAV)
 Facial Sulcus—(MacPhee 1981)
 Facial Vein—Vena facialis (NAV)
 Fenestra Cochleae—(NAV); Fenestra Rotunda (Novacek 1986; Patterson et al. 1989)
 Fenestra Vestibuli—(NAV); Fenestra Ovalis (Novacek 1986; Patterson et al. 1989)
 Fibrous Membrane of Tympanic Cavity—(MacPhee 1981)
 Footplate of Stapes—Basis stapedis (NAV)
 Foramen for Frontal Diploic Vein—(Thewissen 1989); Supraorbital Foramen (Novacek 1986; Gaudin 2004)
 Foramen for Inferior Petrosal Sinus—(Wible 1983); "Foramen for Second Artery" (Patterson et al. 1989)
 Foramen for Ramus Superior—(Wible 1987)
 Foramen magnum—(NAV)
 Foramen ovale—(NAV)
 Foramen rotundum—(Gregory 1910; McDowell 1958)
 Foramen stylomastoideum tertium—(Patterson et al. 1989)
 Foramina for Rami Temporales—(Wible 1987)
 Fossa incudis—(MacPhee 1981)
 Frontal—Os frontale (NAV)
 Frontal Diploic Vein—Vena diploica frontalis (NAV)
 Frontoturbinal—(Reinbach 1952a, 1955)

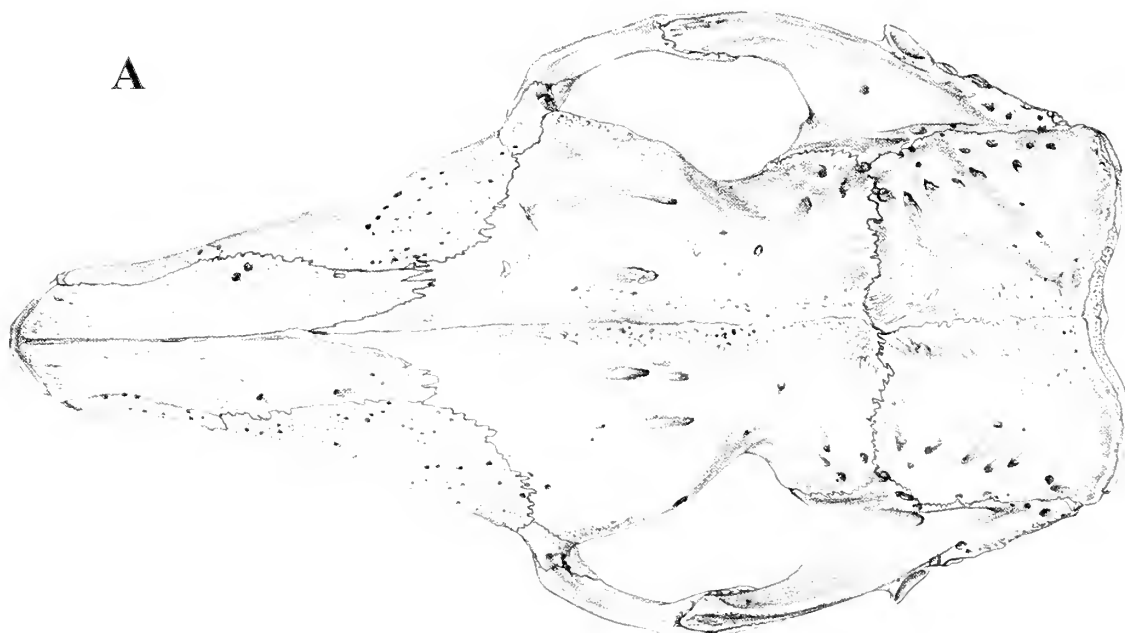
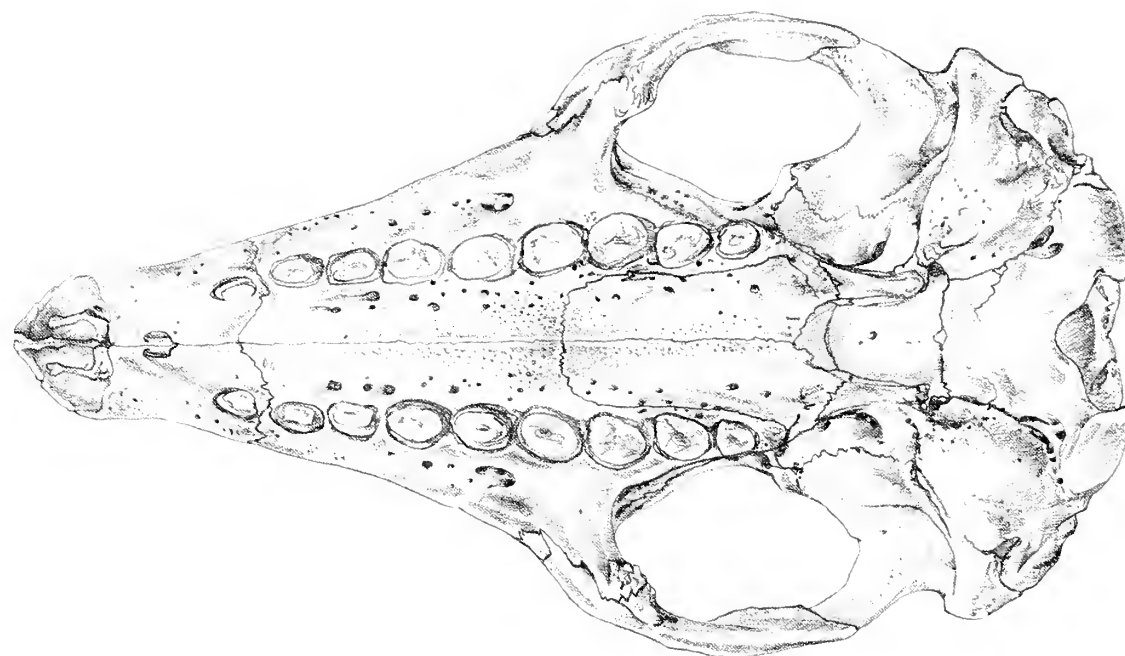
- Geniculate Ganglion—Ganglion geniculi (NAV)
 Genioglossus Muscle—Musculus genioglossus (NAV)
 Geniohyoid Muscle—Musculus geniohyoideus (NAV)
 Gonial—(MacPhee 1981)
 Glaserian Fissure—(Klaauw 1931); Fissura petrotympanica (NAV)
 Glenoid Fossa—Fossa mandibularis (NAV)
 Glossopharyngeal Nerve—Nervus glossopharyngeus (NAV)
 Greater Petrosal Nerve—Nervus petrosus major (NAV)
- Head of Malleus—Caput mallei (NAV)
 Hiatus Fallopii—(Wible 1990); Fallopian Aqueduct (McDowell 1958); Petrosal Canal (Evans 1993)
 Hypoglossal Canal—Canalis nervus hypoglossi (NAV)
 Hypoglossal Foramen—(Evans 1993); Condylar Foramen (Simpson 1931, Gaudin 1995); Condylar Canal (Novacek 1986); Condylar Foramen (Patterson et al. 1989, 1992)
 Hypoglossal Nerve—Nervus hypoglossus (NAV)
 Hypophyseal Fossa—Fossa hypophysialis (NAV)
 Hypophysis—(NAV)
- Incisive Foramen—Fissura palatina (NAV)
 Incus—(NAV)
 Inferior Alveolar Artery—Arteria alveolaris inferior (NAV)
 Inferior Alveolar Nerve—Nervus alveolaris inferior (NAV)
 Inferior Oblique Muscle—Musculus obliquus ventralis (NAV)
 Inferior Petrosal Sinus—Sinus petrosus ventralis (NAV)
 Infraorbital Artery—Arteria infraorbitalis (NAV)
 Infraorbital Canal—Canalis infraorbitalis (NAV)
 Infraorbital Foramen—Foramen infraorbitalis (NAV)
 Infraorbital Nerve—Nervus infraorbitalis (NAV)
 Internal Acoustic Meatus—Meatus acusticus internus (NAV)
 Internal Carotid Artery—Arteria carotis interna (NAV)
 Internal Carotid Nerve—Nervus caroticus interna (NAV)
 Internal Jugular Vein—Vena jugularis interna (NAV)
 Intracranial Foramen of Stapes—Foramen intracraniale (Fleischer 1973)
- Jugal—Os zygomaticum (NAV)
 Jugular Foramen—Foramen jugulare (NAV); Posterior Lacerate Foramen (Simpson 1931; Patterson et al. 1989)
 Jugular Process—Processus jugularis (NAV)
- Lacrimal—Os lacrimale (NAV)
 Lacrimal Fenestra—(Jollie 1968)
 Lacrimal Foramen—Foramen lacrimale (NAV)
 Lacrimal Tubercle—(Novacek 1986)
 Lamina anterior transversalis—(Reinbach 1952a, 1952b, 1955)
 Lamina of Malleus—(Henson 1961)
 Lamina parietalis—(Reinbach 1952a, 1952b, 1955)
 Lateral Process of Malleus—Malleus, Processus lateralis (NAV)
 Lateral Pterygoid Muscle—Musculus pterygoideus lateralis (NAV)
 Lesser Petrosal Nerve—Nervus petrosus minor (NAV)
 Levator Hyoidei Muscle—(Edgeworth 1931, 1935)
 Levator palpebrae superioris—(NAV)
 Levator Veli Palatini—Musculus levator veli palatini (NAV)
 Longus Capitis Muscle—Musculus longus capitis (NAV)
- Major Palatine Artery—Arteria palatina major (NAV)
 Major Palatine Foramen—Foramen palatinum majus (NAV); Anterior Palatine Foramen (Novacek 1986)
 Major Palatine Nerve—Nervus palatinus major (NAV)
 Malleus—(NAV)
 Mandible—Mandibula (NAV)
 Mandibular Canal—Canalis mandibulae (NAV)
 Mandibular Foramen—Foramen mandibulae (NAV); Dental Foramen (Simpson 1931)
 Mandibular Nerve—Nervus mandibularis (NAV)
 Mandibular Sulci—New term
 Mandibular Symphysis—(Evans 1993)
- Mandibulo-auricularis Muscle—(Uekermann 1912)
 Manubrium of Malleus—Manubrium mallei (NAV)
 Masseter Muscle—Musculus masseter (NAV)
 Mastoid Exposure of Petrosal—Mastoid Process (Evans 1993)
 Mastoid Foramen—Foramen mastoideum (NAV)
 Mastoideostyloideus—(Saban 1968)
 Maxilla—(NAV)
 Maxillary Artery—Arteria maxillaris (NAV); Ramus infraorbitalis (Wible 1987)
 Maxillary Foramen—Foramen maxillare (NAV)
 Maxillary Nerve—Nervus maxillaris (NAV)
 Maxillary Recess—Recessus maxillaris (NAV)
 Maxillary Tuberosity—Tuber maxillae (NAV)
 Maxillonasolabialis—(Edgeworth 1935)
 Maxilloturbinal—Os conchae nasalis ventralis (NAV)
 Meckelian Groove—(Bensley 1902)
 Meckel's Cartilage—(De Beer 1937; MacPhee 1981)
 Medial Pterygoid Muscle—Musculus pterygoideus medialis (NAV)
 Mental Artery—Arteria mentalis (NAV)
 Mental Foramen—Foramen mentale (NAV)
 Mental Nerve—Nervus mentalis (NAV)
 Mentalis Muscle—Musculus mentalis (NAV)
 Middle Meningeal Artery—Arteria meningea media (NAV)
 Minor Palatine Artery—Arteria palatina minor (NAV)
 Minor Palatine Foramen—Foramen palatinum caudale (NAV)
 Minor Palatine Nerve—Nervus palatinus minor (NAV)
 Muscular Process of Malleus—Malleus, Processus muscularis (NAV)
 Muscular Process of Stapes—(Evans 1993)
 Musculotubal Canal—Canalis musculotubarius (NAV); Eustachian Foramen (Simpson 1931); Eustachian Tube Opening (Patterson et al. 1989)
 Mylohyoid Muscle—Musculus mylohyoideus (NAV)
 Mylohyoid Nerve—Nervus mylohyoideus (NAV)
 Mylohyoid Sulcus—Sulcus mylohyoideus (NAV)
- Nasal—Os nasale (NAV)
 Nasal Foramen—(Simpson 1937)
 Nasal Septum—Septum nasi osseum (NAV)
 Nasalis Muscle—(Uekermann 1912)
 Nasolacrimal Duct—Ductus nasolacrimalis (NAV)
 Nasopalatine Duct—Ductus nasopalatinus (NAV)
 Nasopalatine Nerve—Nervus nasopalatinus (NAV)
 Nasopharyngeal Duct—Ductus nasopharyngeus (Reinbach 1952a, 1955); Meatus nasopharyngeus (NAV)
 Nasoturbinal—(Evans 1993)
 Neck of Malleus—(Henson 1961)
 Nerve of Pterygoid Canal—Nervus canalis pterygoidei (NAV)
 Nerve to Stapedius Muscle—Nervus stapedius (NAV)
 Nuchal Crest—Crista nuchae (NAV)
- Occipital Artery—Arteria occipitalis (NAV)
 Occipital Condyle—Condylus occipitalis (NAV)
 Occipital Emissary Vein—Vena emissaria occipitalis (NAV)
 Occipital Groove—Sulcus arteria occipitalis (Nomina Anatomica); Mastoid Groove (Patterson et al. 1989)
 Oculomotor Nerve—Nervus oculomotorius (NAV)
 Odontoid Notch—Intercondyloid Notch (Evans 1993)
 Ophthalmic Artery—Arteria ophthalmica interna (NAV)
 Ophthalmic Nerve—Nervus ophthalmica (NAV)
 Optic Foramen—Canalis opticus (NAV)
 Optic Nerve—Nervus opticus (NAV)
 Orbito-auricular Muscle—(Uekermann 1912)
 Orbitosphenoid—Os presphenoidale, Ala (NAV)
 Orbitotemporal Canal—(Rougier et al. 1992); Sinus Canal (McDowell 1958); Cranio-orbital Foramen (MacPhee 1994)
 Orbitotemporal Fossa—Orbita + Fossa temporalis (NAV)
 Os lenticulare—(NAV)
 Otic Ganglion—Ganglion oticum (NAV)

- Palatine—Os palatinum (NAV)
 Palatine Canal—Canalis palatinus major (NAV)
 Paracondylar Process—Processus Paracondylaris (NAV); Paroccipital Process (Novacek 1986; Patterson et al. 1989; MacPhee 1994)
 Parietal—Os parietale (NAV)
 Parietal Foramen—(Boyd 1930)
 Paroccipital Process—(Rougier et al. 1992); Mastoid Process (Patterson et al. 1989)
 Pars canalicularis—(Wible 1990); Pars Mastoidea (Patterson et al. 1989)
 Pars cochlearis—(Wible 1990); Pars Petrosa (Patterson et al. 1989)
 Perilymphatic Duct—Ductus perilymphaticus (NAV)
 Perpendicular Plate of Ethmoid—Os ethmoidale, Lamina perpendicularis (NAV)
 Petrosal—Os temporale, Pars petrosa (NAV)
 Petrotympanic Fissure—Fissura petrotympanica (NAV)
 Piriform Fenestra—(MacPhee 1981); Foramen lacerum (NAV); Foramen lacerum medium (Patterson et al. 1989)
 Pharynx—(NAV)
 Posterior Digastric Muscle—Musculus digastricus, Venter caudalis (NAV)
 Postglenoid Foramen—Foramen retroarticulare (NAV)
 Postglenoid Process—Processus retroarticulare (NAV)
 Postorbital Process—Os frontale, Processus zygomaticus (NAV)
 Postpalatine Torus—(Novacek 1986a)
 Post-promontorial Tympanic Sinus—(Wible 1990)
 Posttemporal Canal—(Rougier et al. 1992); Mastoid Foramen (Patterson et al. 1989, 1992); Petrosal Canal (MacPhee 1994)
 Posttympanic Process—(Novacek 1986)
 Premaxilla—Os incisivum (NAV)
 Presphenoid—Os presphenoidale, Corpus (NAV)
 Primary Facial Foramen—(Wible 1990)
 "Processus cristae facialis"—(Patterson et al. 1989)
 Promontorium of Petrosal—(Evans 1993)
 Pterygoid—Os pterygoideum (NAV)
 Pterygoid Canal—Canalis pterygoideus (NAV); Vidian Canal (MacPhee 1994)
 Pterygopalatine Ganglion—Ganglion pterygopalatinum (NAV)
- Ramus of Mandible—Ramus mandibular (NAV)
 Ramus Orbitalis—(Wible 1987)
 Ramus Inferior of Stapedial Artery—(Wible 1987)
 Ramus Superior of Stapedial Artery—(Wible 1987)
 Ramus Supraorbitalis—(Wible 1987)
 Ramus Temporalis—(Wible 1987)
 Rathke's Pouch—(Clemente 1985)
 Recessus meatus—(McDowell 1958)
 Reichert's Cartilage—(De Beer 1937; MacPhee 1981)
 Rectus Capitis Ventralis Muscle—Musculus rectus capitis ventralis (NAV)
 Rostral Tympanic Artery—Arteria tympanica rostralis (NAV)
- Sacculi—Sacculus (NAV)
 Secondary Facial Foramen—(Wible 1990); Stylo mastoid Foramen (Primitivum) (Novacek 1986)
 Secondary Tympanic Membrane—Membrana tympani secundaria (NAV)
 Semicircular Canal—Canalis semicircularis (NAV)
 Septomaxilla—(Wible et al. 1990)
 Sigmoid Sinus—Sinus sigmoideus (NAV)
 Sphenorbital Fissure—(Novacek 1986); Fissura orbitalis (NAV); Anterior Lacerate Foramen (Simpson 1931); Sphenoid Fissure (Patterson et al. 1989); Spheno-orbital Fissure (MacPhee 1994); Superior Orbital Fissure (Wible et al. 2004)
 Sphenopalatine Artery—Arteria sphenopalatina (NAV)
 Sphenopalatine Foramen—Foramen sphenopalatinum (NAV)
 Splenius Capitis Muscle—Musculus splenius capitis (NAV)
 Squamosal—Os temporale, Pars squamosa (NAV)
- Stapedial Artery—(Wible 1987)
 Stapedius Fossa—(MacPhee 1981)
 Stapedius Muscle—Musculus stapedius (NAV)
 Stapes—(NAV)
 Sternomastoid Muscle—Musculus sternomastoideus (NAV)
 Stylohyal—Stylohyoideum (NAV)
 Stylohyal Fossa—(Patterson et al. 1992)
 Stylo mastoid Artery—Arteria stylo mastoidea
 Stylo mastoid Foramen—Foramen stylo mastoideum (NAV); Stylo mastoid Foramen (Definitivum) (Novacek 1986)
 Stylopharyngeus Muscle—Musculus stylopharyngeus caudalis (NAV)
 Sublingual Artery—Arteria sublingualis (NAV)
 Subsquamosal Foramen—(Wible et al. 2004); Squamosal Sinus—Canal (Novacek 1986)
 Sulcus tympanicus—(NAV)
 Superficial Masseter Muscle—(Evans 1993)
 Superior Alveolar Rami—Nervus infraorbitalis, Rami alveolares superiores (NAV)
 Superior Petrosal Sinus—Sinus petrosus dorsalis (NAV)
 Superior Pharyngeal Constrictor—Musculus hyopharyngeus (NAV)
 Suprameatal Bridge—Dorsal Boundary of External Acoustic Meatus (Evans 1993)
 Suprameatal Foramen—(Novacek 1986)
 Supraoccipital—Squama occipitalis (NAV)
 Supraoccipital Foramina—(Wible et al. 2004)
- Tectum nasi—(Reinbach 1952a, 1955)
 Tectum synoticum—(De Beer 1937; Reinbach 1952a, 1955)
 Tegmen tympani—(NAV)
 Temporal Fascia—Fascia temporalis (NAV)
 Temporal Fossa—Fossa temporalis (NAV)
 Temporal Line—Linea temporalis (NAV)
 Temporalis Muscle—Musculus temporalis (NAV)
 Temporomandibular Joint—Articulatio temporomandibularis (NAV)
 Tensor Tympani Muscle—Musculus tensor tympani (NAV)
 Tensor Veli Palatini—Musculus tensor veli palatini (NAV)
 Transverse Canal Foramen—(Sánchez-Villagra and Wible 2002); Transverse Sinus (MacPhee 1994)
 Transverse Sinus—Sinus transversus (NAV)
 Trigeminal Ganglion—Ganglion trigeminale (NAV)
 Trigeminal Nerve—Nervus trigeminus (NAV)
 Trochlear Nerve—Nervus trochlearis (NAV)
 Tympanic Cavity—Cavum tympani (NAV)
 Tympanic Membrane—Tympanum (NAV)
 Tympanic Process of Alisphenoid—(MacPhee 1981); Preotic Crest of Alisphenoid (Novacek 1986)
 Tympanic Process of Pterygoid—(MacPhee 1981)
 Tympanohyal—Tympanohyoideum (NAV); Mastoid Tubercle (Novacek 1986)
- Utricle—Utriculus (NAV)
- Vagus Nerve—Nervus vagus (NAV)
 Ventral Condylar Foramina—New term
 Ventral Condylar Fossa—Fossa condylaris ventralis (NAV)
 Vestibular Fossula—(MacPhee 1981)
 Vomer—(NAV)
 Vomer nasal Cartilage—Cartilago vomeronasalis (NAV)
 Vomer nasal Organ—Organum vomeronasale (NAV)
- Zygoma—Arcus zygomaticus (NAV)
 Zygomatic Portion of Platyssa—(Uekermann 1912)
 Zygomatic Process of Maxilla—Maxilla, Processus zygomaticus (NAV)
 Zygomatic Process of Squamosal—Os temporale, Pars squama, Processus zygomaticus (NAV)

TABLE 1. *Cranial Measurements (mm) of Euphraetus sexcinctus*

	FMNH 28350	CM 6398	CM 6399	CM 10742	CM 61426	CM 101007
ONL	113.6	119.9	122.4	98.9	116.9	105.9
POL	54.2	57.0	54.5	43.7	57.2	48.7
PL	66.0	67.1	69.9	50.0	63.4	59.2
PPL	35.5	41.5	35.7	31.0	35.8	33.5
PB	23.4	23.9	25.3	19.8	24.3	22.6
ZB	63.8	72.8	71.5	52.6	65.9	59.5
IB	25.8	27.1	25.9	24.3	25.6	24.8
MB	50.5	55.6	56.6	44.6	52.7	49.3
ML	87.1	92.3	94.5	70.8	86.8	83.2
MD	13.7	14.4	13.6	9.4	13.8	11.1
CH	33.0	33.0	33.4	27.6	36.1	34.7
CPH	14.4	16.3	17.6	11.4	13.9†	14.0
LTRL	55.7	57.4	58.4	45.6	55.0	49.1
UTRL	52.5	53.6	53.3	41.1	51.3	47.0

Mandibular measurements and tooth row lengths on right side; †estimated. Abbreviations: **CH**, ascending ramus height at condyle; **CPH**, coronoid process height from mandibular notch; **IB**, interorbital breadth; **LTRL**, lower tooth row length; **MB**, mastoid breadth; **MD**, mandibular body depth at eighth tooth; **ML**, mandible length; **ONL**, occipitonasal length; **PB**, palatal breadth at fifth maxillary tooth; **PL**, palatal length; **POL**, pre-orbital length; **PPL**, postpalatal length; **UTRL**, upper tooth row length; **ZB**, greatest zygomatic breadth.

A**B**

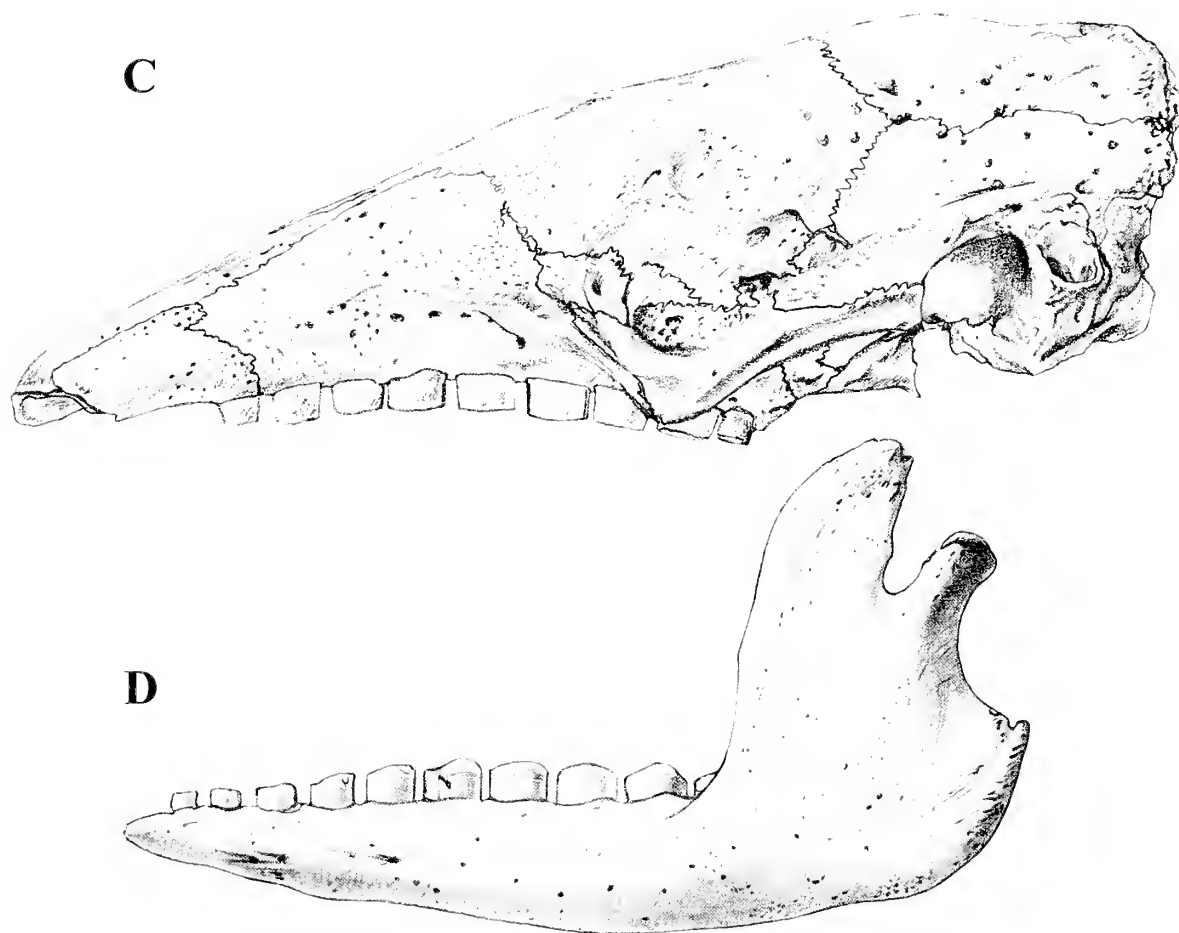
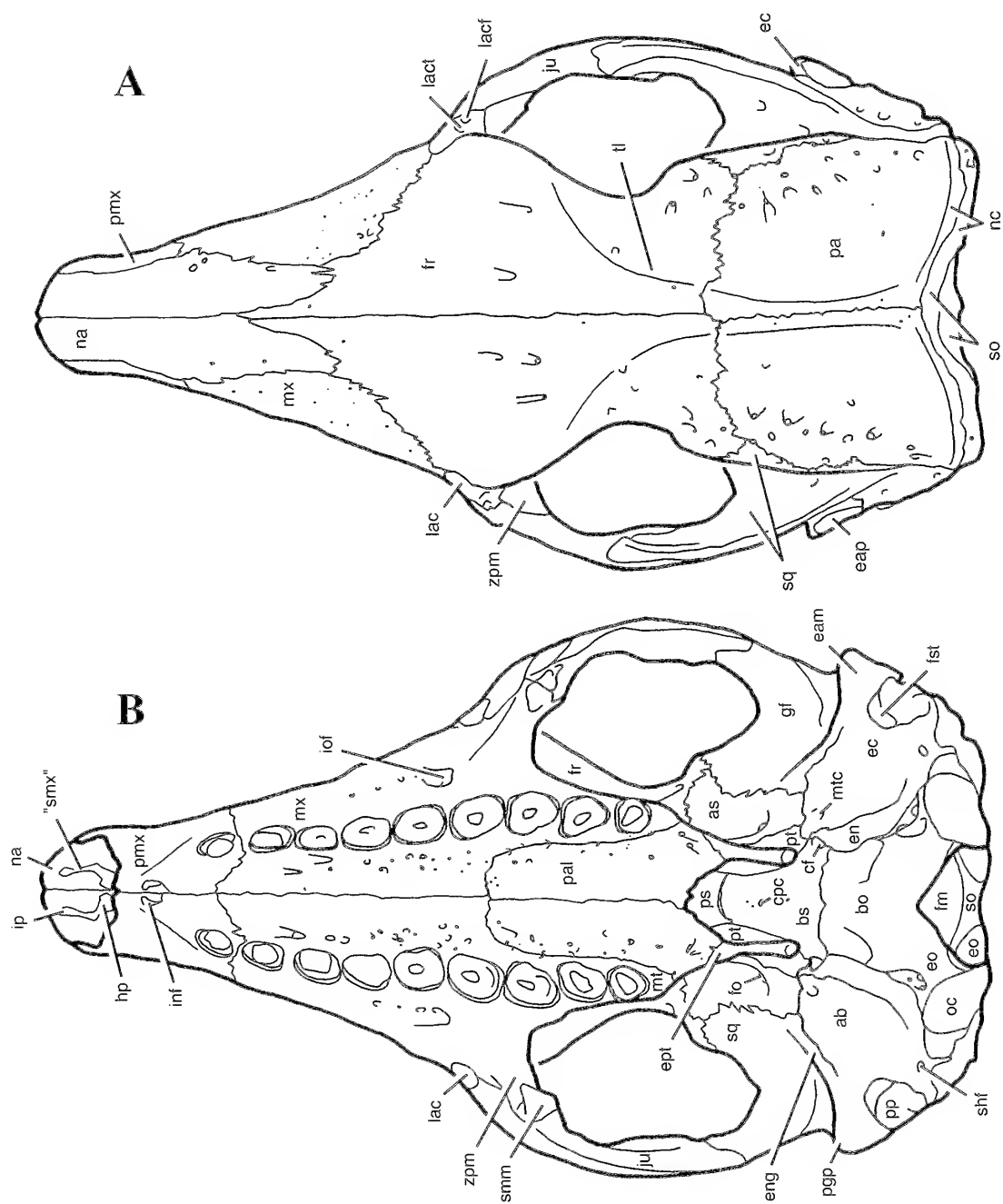


Fig. 1—*Euphractus sexcinctus* FMNH 28350, skull in dorsal (A), ventral (B), and left lateral (C) views and left mandible in lateral (D) view. Line drawings of these views with labeled structures and scales are in Figs. 2 and 7A. Part of the right auditory bulla is removed from the specimen, but is reconstructed here based on the left side. The cartilaginous nasal septum is preserved in the specimen and is visible in the ventral and lateral views, but is not shown in the accompanying line drawings.



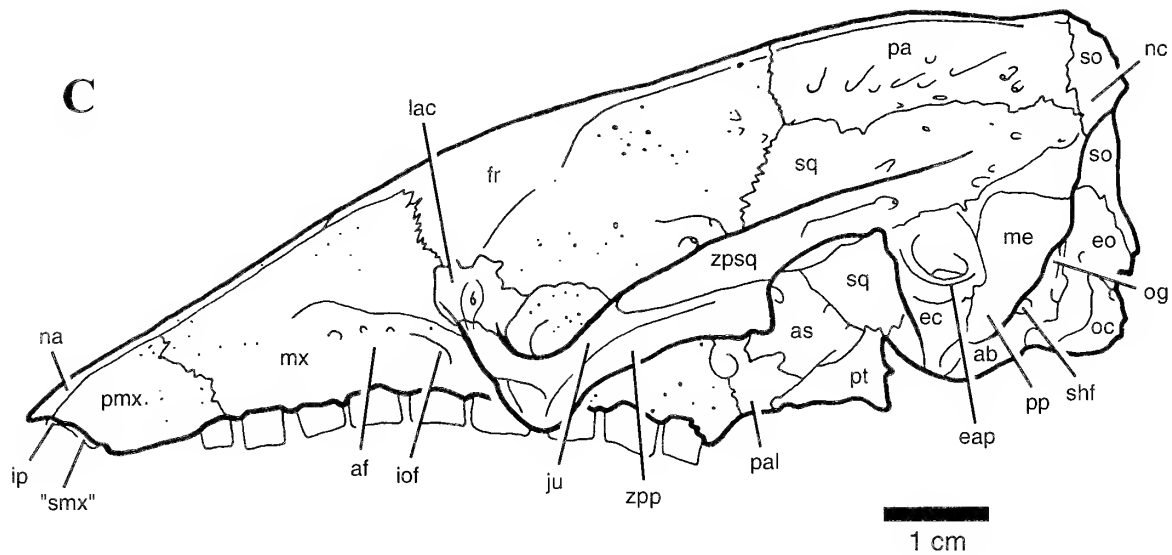


Fig. 2—*Euphractus sexcinctus* FMNH 28350, line drawings of skull in dorsal (A), ventral (B), and left lateral (C) views. Abbreviations: **ab**, auditory bulla; **af**, antorbital fossa; **as**, alisphenoid; **bo**, basioccipital; **bs**, basisphenoid; **cf**, carotid foramen; **epe**, craniopharyngeal canal; **eam**, external acoustic meatus; **eap**, external acoustic porus; **ec**, ectotympanic; **en**, entotympanic; **eng**, entoglenoid process of the squamosal; **eo**, exoccipital; **ept**, entopterygoid crest; **fst**, foramen stylomastoideum tertium; **hp**, horizontal process of the "septomaxilla"; **inf**, incisive foramen; **fo**, foramen ovale; **fr**, frontal; **iof**, infraorbital foramen; **ip**, interfenestral process of the "septomaxilla"; **ju**, jugal; **lac**, lacrimal; **laef**, lacrimal foramen; **laet**, lacrimal tubercle; **me**, mastoid exposure of the petrosal; **mtc**, musculotubal canal; **mx**, maxilla; **mxt**, maxillary tuberosity; **na**, nasal; **nc**, nuchal crest; **oc**, occipital condyle; **og**, occipital groove; **pa**, parietal; **pal**, palatine; **pdp**, postglenoid process (based on CM 10743); **pmx**, premaxilla; **pp**, paroccipital process of the petrosal; **ps**, presphenoid; **pt**, pterygoid; **shf**, stylohyal fossa; **smm**, superficial masseter muscle; **"smx"**, septomaxilla; **so**, supraoccipital; **sq**, squamosal; **tl**, temporal line; **zpm**, zygomatic process of the maxilla; **zpp**, zygomatic portion of the platysma muscle; **zpsq**, zygomatic process of the squamosal.

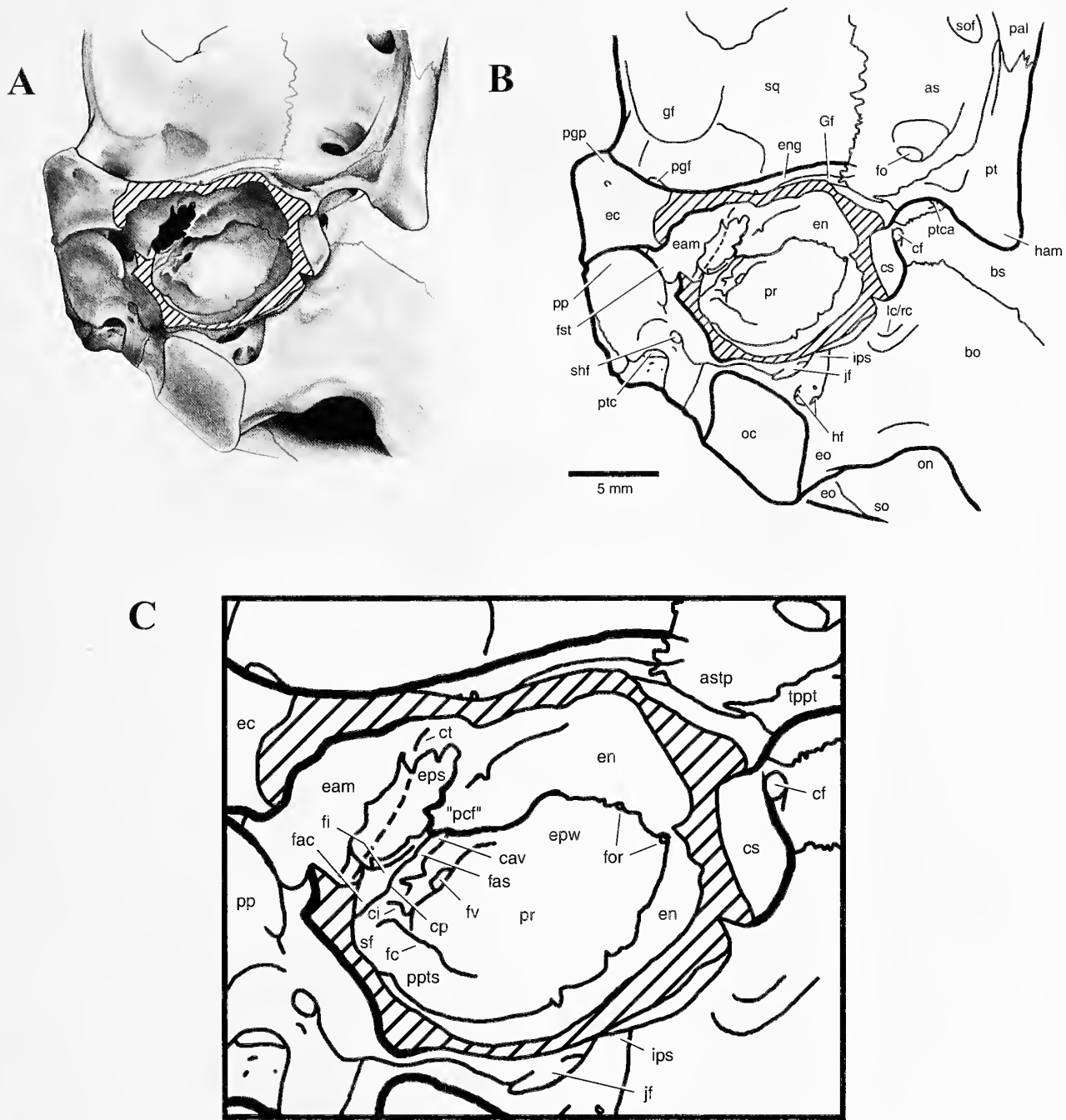


Fig. 4—*Euphractus sexcinctus* FMNH 28350, right basicranium in oblique ventral view (A), with accompanying line drawing (B), and close up of the ear region (C). Parallel lines represent cut surfaces. Dashed line is our reconstruction of the damaged ectotympanic. Abbreviations: **as**, alisphenoid; **astp**, alisphenoid tympanic process; **bo**, basioccipital; **bs**, basisphenoid; **cav**, cavum supracochleare; **cf**, carotid foramen; **ci**, crista interfenestralis; **cp**, crista parotica; **cs**, carotid sulcus; **ct**, crista tympanica; **eam**, external acoustic meatus; **ec**, ectotympanic; **en**, entotympanic; **eng**, entoglenoid process of the squamosal; **eo**, exoccipital; **eps**, epitympanic sinus; **epw**, epitympanic wing of the petrosal; **fac**, facial canal; **fas**, facial sulcus; **fc**, fenestra cochleae; **fi**, fossa incudis; **fm**, foramen magnum; **fo**, foramen ovale; **for**, unnamed foramina; **fst**, foramen stylomastoideum tertium; **fv**, fenestra vestibuli; **Gf**, Glaserian fissure; **gf**, glenoid fossa; **ham**, hamulus; **hf**, hypoglossal foramen; **jf**, jugular foramen; **lc/rc**, longus capitus/rectus capitus fossa; **oc**, occipital condyle; **on**, odontoid notch; **pal**, palatine; **"pcf"**, "processus cristae facialis"; **pgf**, postglenoid foramen; **pgp**, postglenoid process (based on CM 10743); **pp**, paroccipital process of the petrosal; **ppts**, post-promontorial tympanic sinus; **pr**, promontorium of the petrosal; **pt**, pterygoid; **ptc**, posttemporal canal, posterior opening; **ptca**, pterygoid groove enclosed to form a canal; **pttp**, pterygoid tympanic process; **sf**, stapedius fossa; **shf**, stylohyal fossa; **so**, supraoccipital; **sof**, sphenorbital fissure; **spf**, sphenopalatine foramen; **sq**, squamosal.

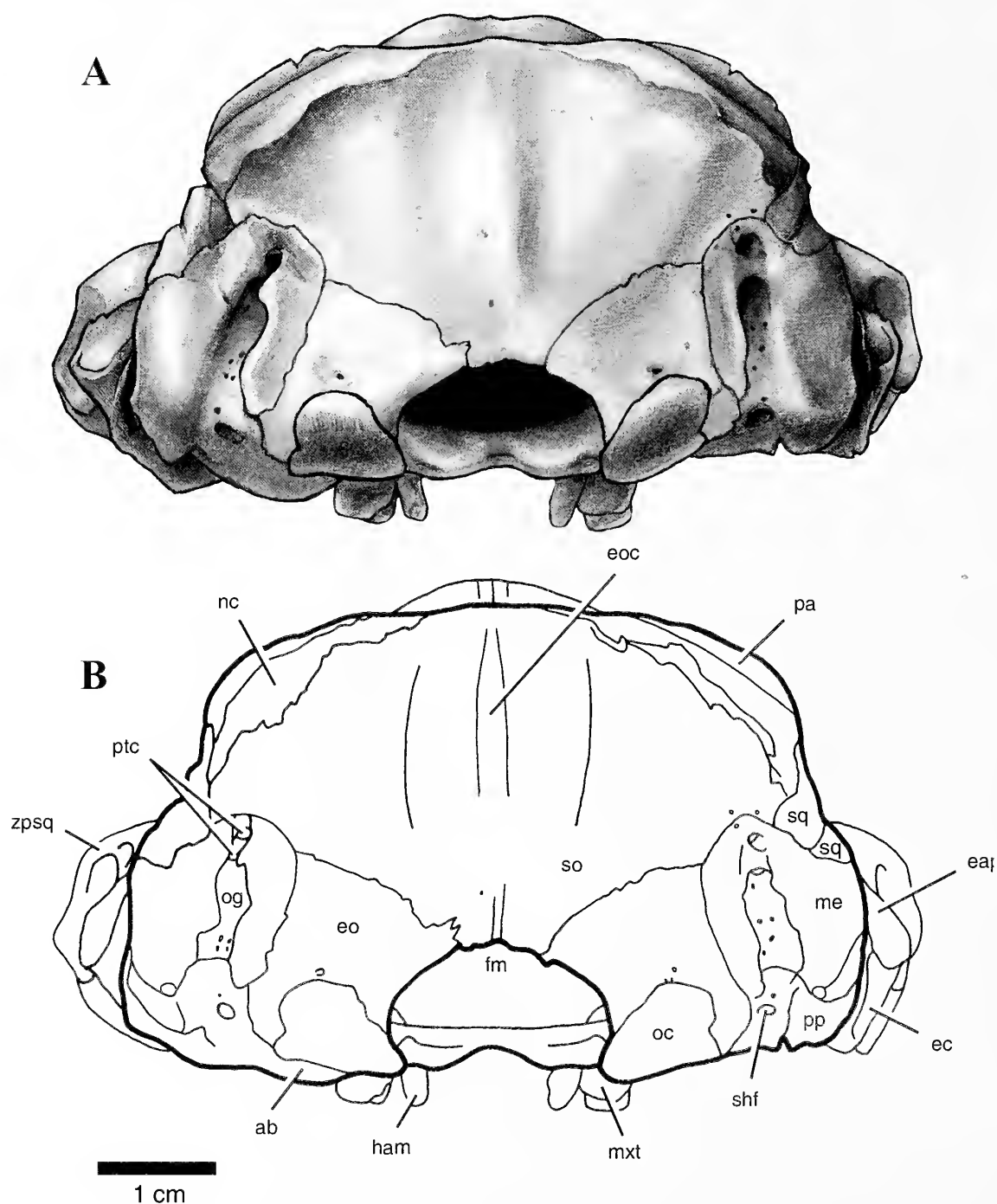


Fig. 5—*Euphractus sexcinctus* FMNH 28350, occiput (A), with accompanying line drawing (B). Abbreviations: **ab**, auditory bulla; **eap**, external acoustic porus; **ec**, ectotympanic; **eo**, exoccipital; **eoc**, external occipital crest; **fm**, foramen magnum; **ham**, hamulus; **me**, mastoid exposure of the petrosal; **mxt**, maxillary tuberosity; **nc**, nuchal crest; **oc**, occipital condyle; **og**, occipital groove; **pa**, parietal; **pp**, paroccipital process of the petrosal; **ptc**, posttemporal canal, posterior opening; **shf**, stylohyal fossa; **so**, supraoccipital; **sq**, squamosal; **zpsq**, zygomatic process of the squamosal.

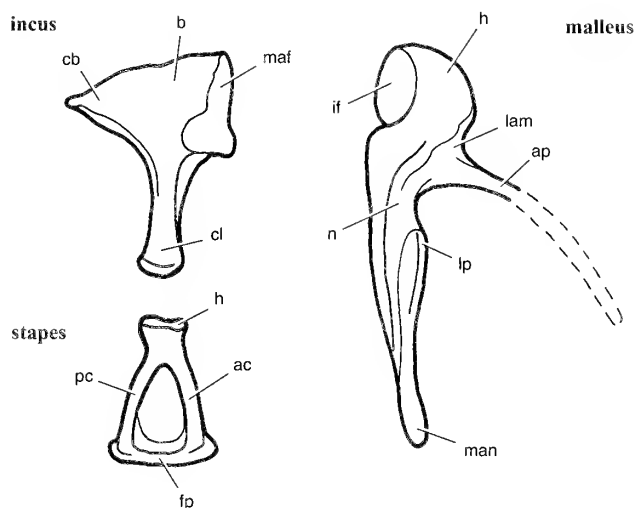


Fig. 6—*Euphractus sexcinctus*, line drawing of right malleus, incus, and stapes redrawn from Guth (1961: fig. 87). Abbreviations: **ac**, anterior crus; **ap**, anterior process; **b**, body; **cb**, crus breve; **cl**, crus longum; **fp**, footplate or base; **h**, head; **if**, incudal facet on the malleus; **lam**, lamina; **lp**, lateral process; **man**, manubrium; **maf**, malleolar facet on the incus; **n**, neck; **pc**, posterior crus.

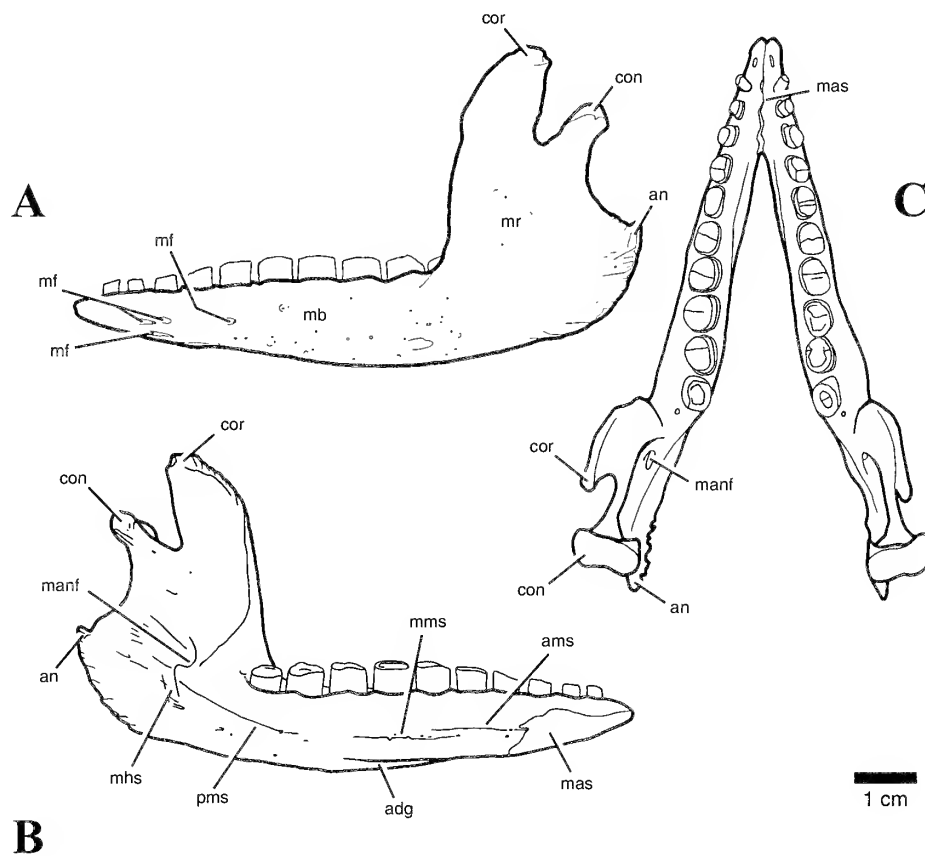


Fig. 7—*Euphractus sexcinctus* FMNH 28350, line drawing left mandible in lateral (A), medial (B), and occlusal (C) views. Abbreviations: **adg**, attachment for anterior digastric muscle; **ams**, anterior mandibular sulcus; **an**, angular process; **con**, condylar process; **cor**, coronoid process; **manf**, mandibular foramen; **mas**, mandibular symphysis; **mb**, mandibular body; **mf**, mental foramina; **mhs**, mylohyoid sulcus; **mms**, middle mandibular sulcus; **mr**, mandibular ramus; **pms**, posterior mandibular sulcus.

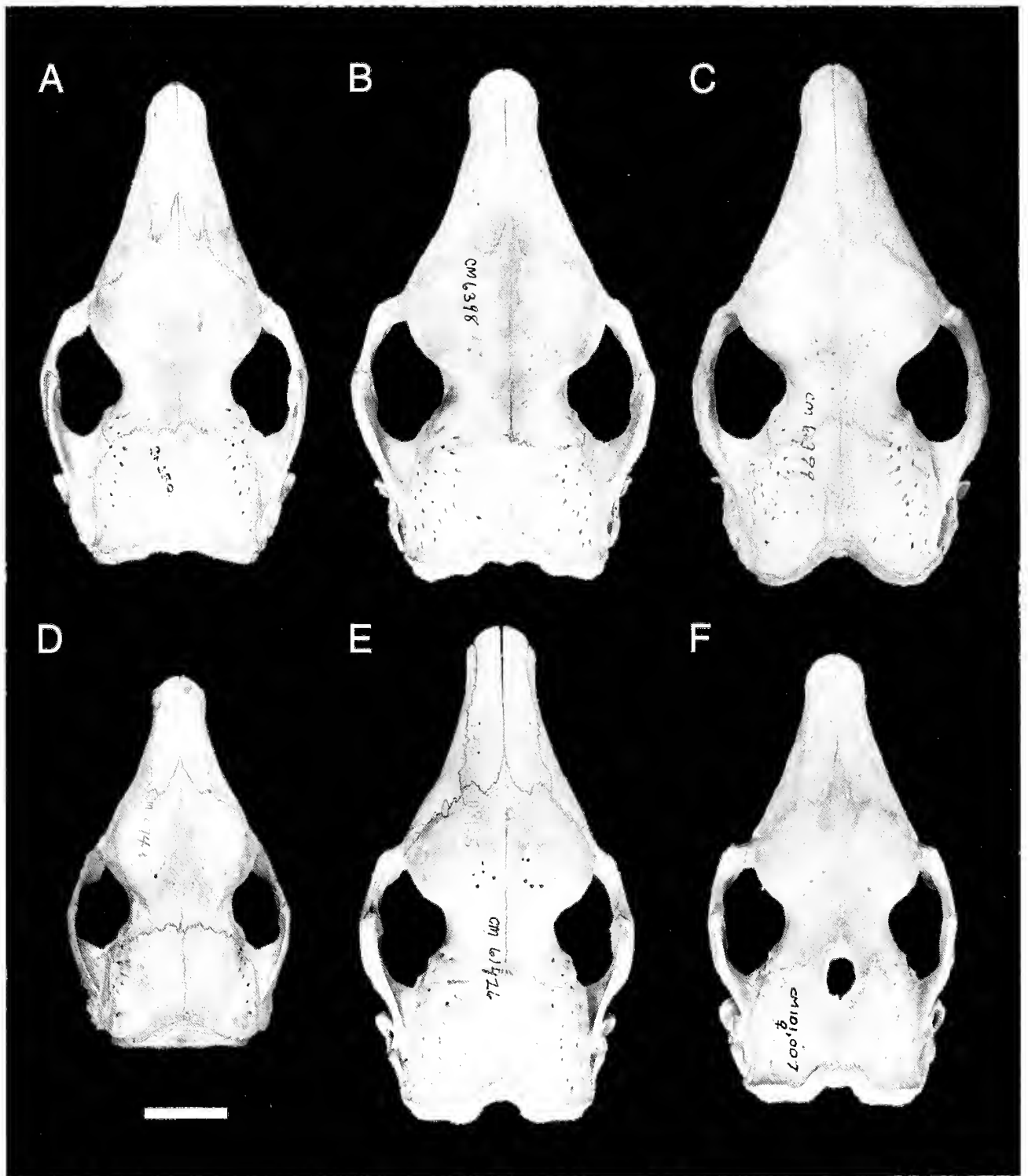


Fig. 8—*Euphractus sexcinctus*, skulls in dorsal view: FMNH 28350 (A), CM 6398 (B), CM 6399 (C), CM 10743 (D), CM 61426 (E), and CM 101007 (F). Scale = 2 cm.

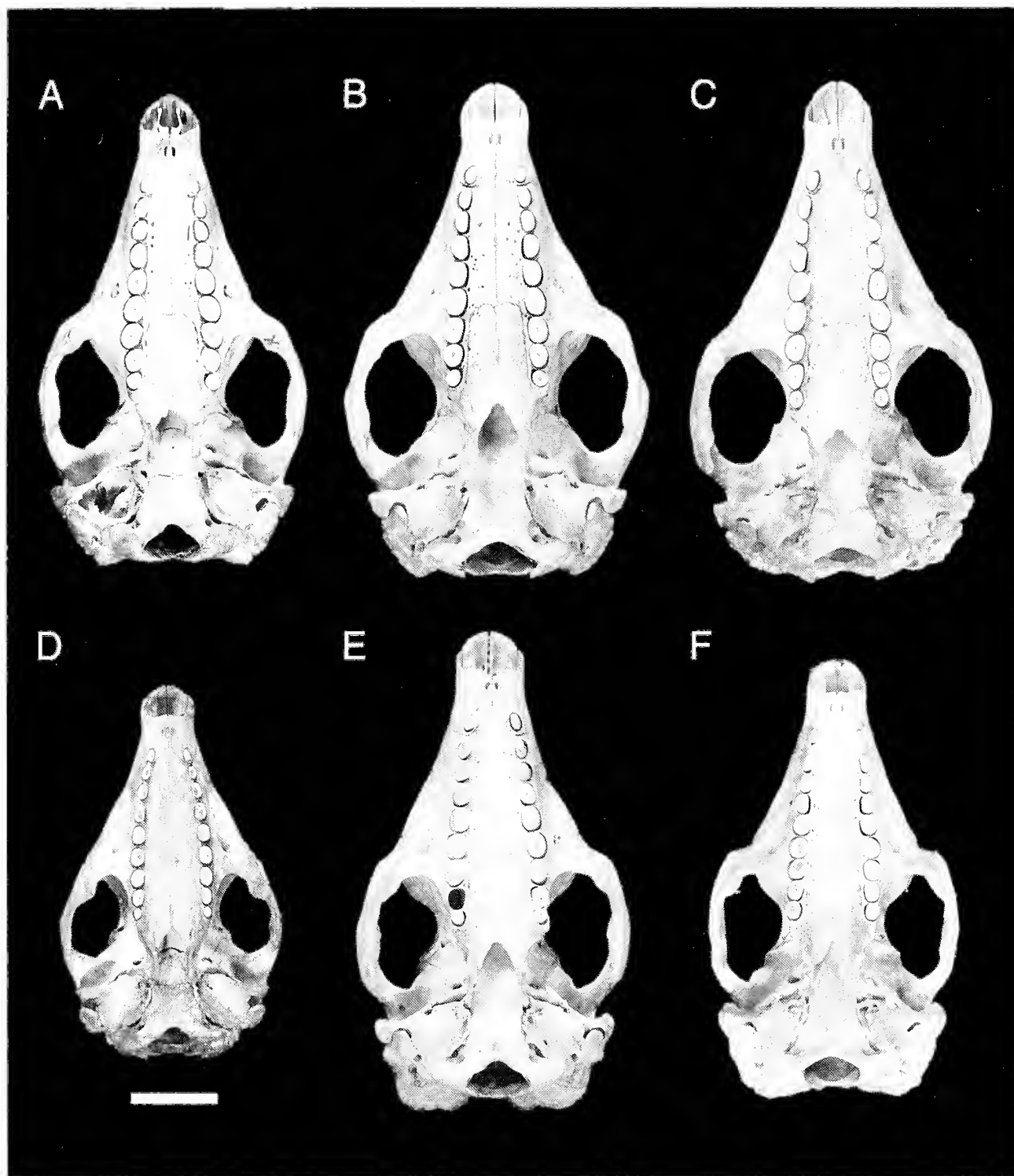


Fig. 9—*Euphractus sexcinctus*, skulls in ventral view: FMNH 28350 (A), CM 6398 (B), CM 6399 (C), CM 10743 (D), CM 61426 (E), and CM 101007 (F). Scale = 2 cm.

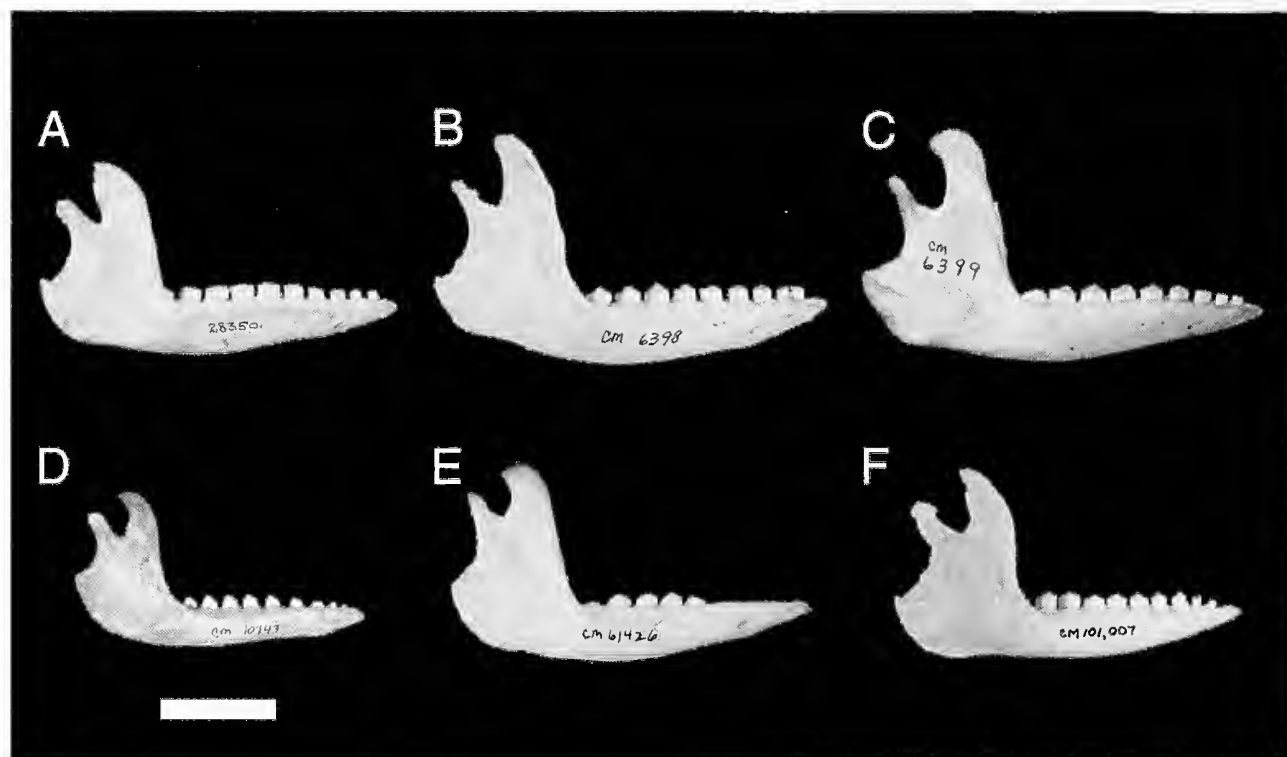


Fig. 10—*Euphractus sexcinctus*, right mandibles in lateral view: FMNH 28350 (A), CM 6398 (B), CM 6399 (C), CM 10743 (D), CM 61426 (E), and CM 101007 (F). Scale = 2 cm.

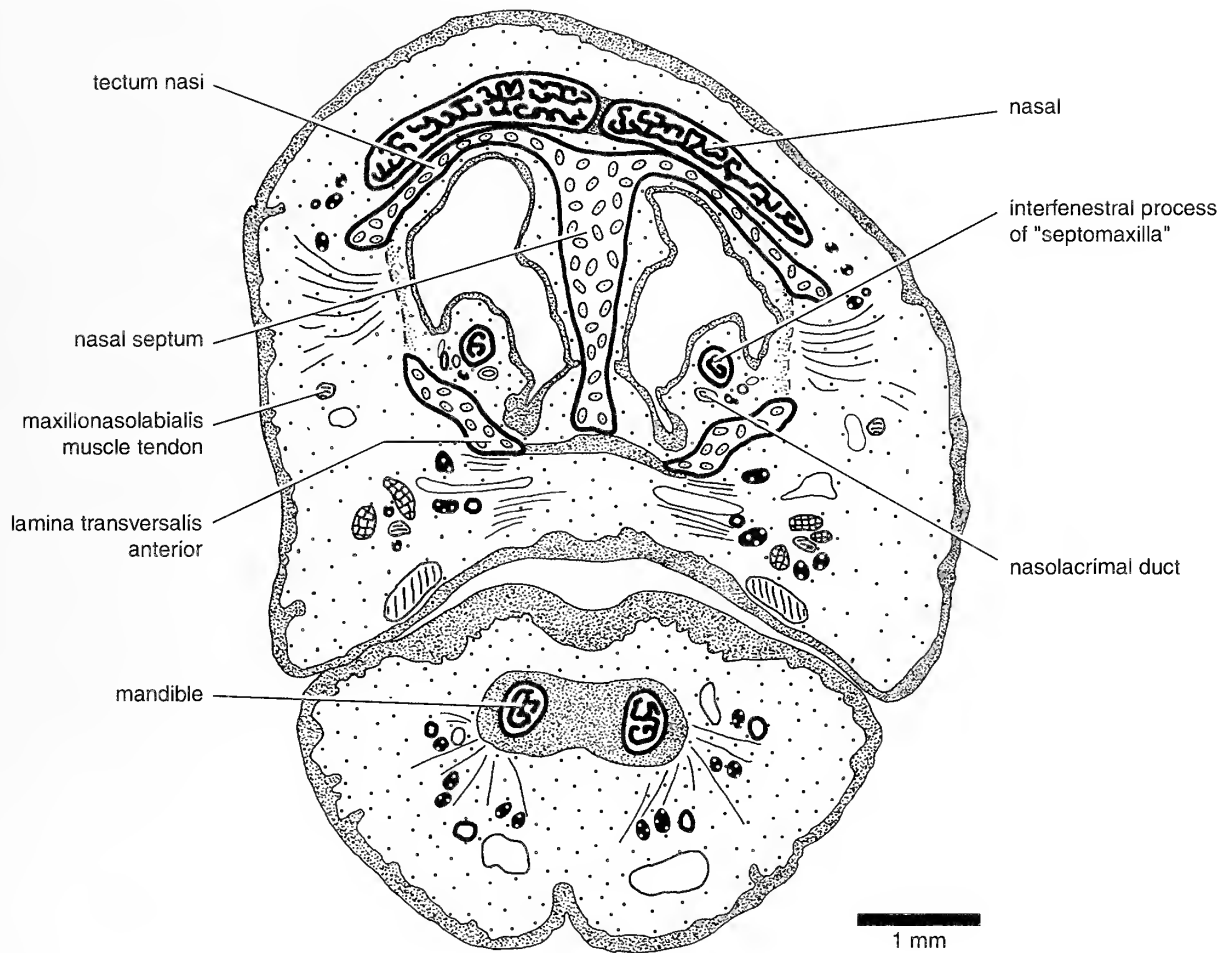


Fig. 11—*Euphractus sexcinctus* FMNH E28532, schematic representation of slide 888-3, a frontal section through the anterior tip of the snout. Omitted from this simplified figure are dozens of small nerves and muscle fibers in the ventrolateral part of both the upper and lower jaws. See Reinbach (1955) for descriptions and reconstructions of the nasal cartilages in a fetus of the euphractine *Zaedyus minutus*.

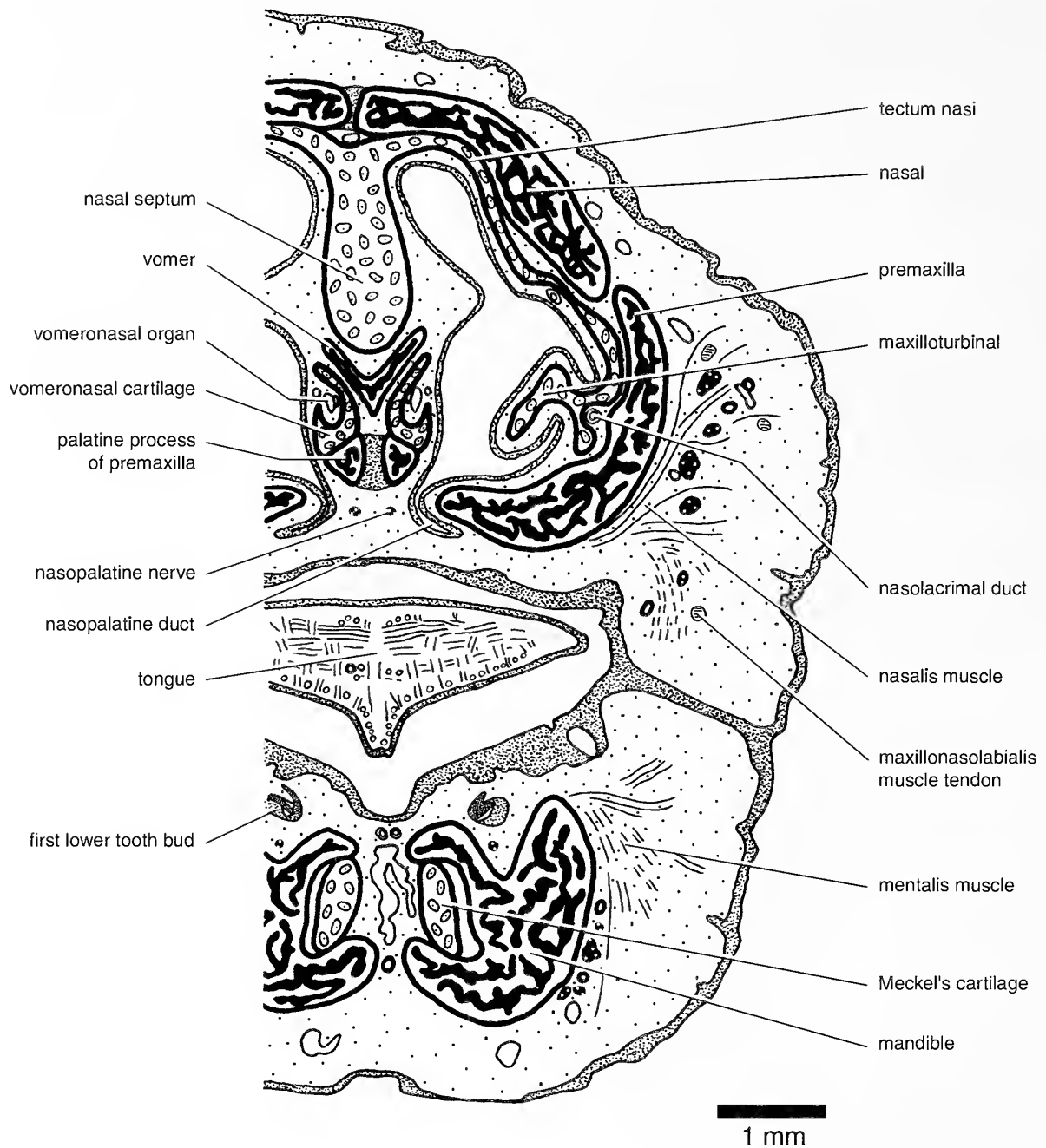


Fig. 12—*Euphractus sexcinctus* FMNH E28532, schematic representation of part of slide 838-2, a frontal section through the snout at the level of the incisive foramen. In the upper jaw, branches of the infraorbital nerve and vessels, and tendons of the maxillonasolabialis muscle run through the nasalis muscle and in the lower jaw, branches of the mental nerve and vessels run through the mentalis muscle.

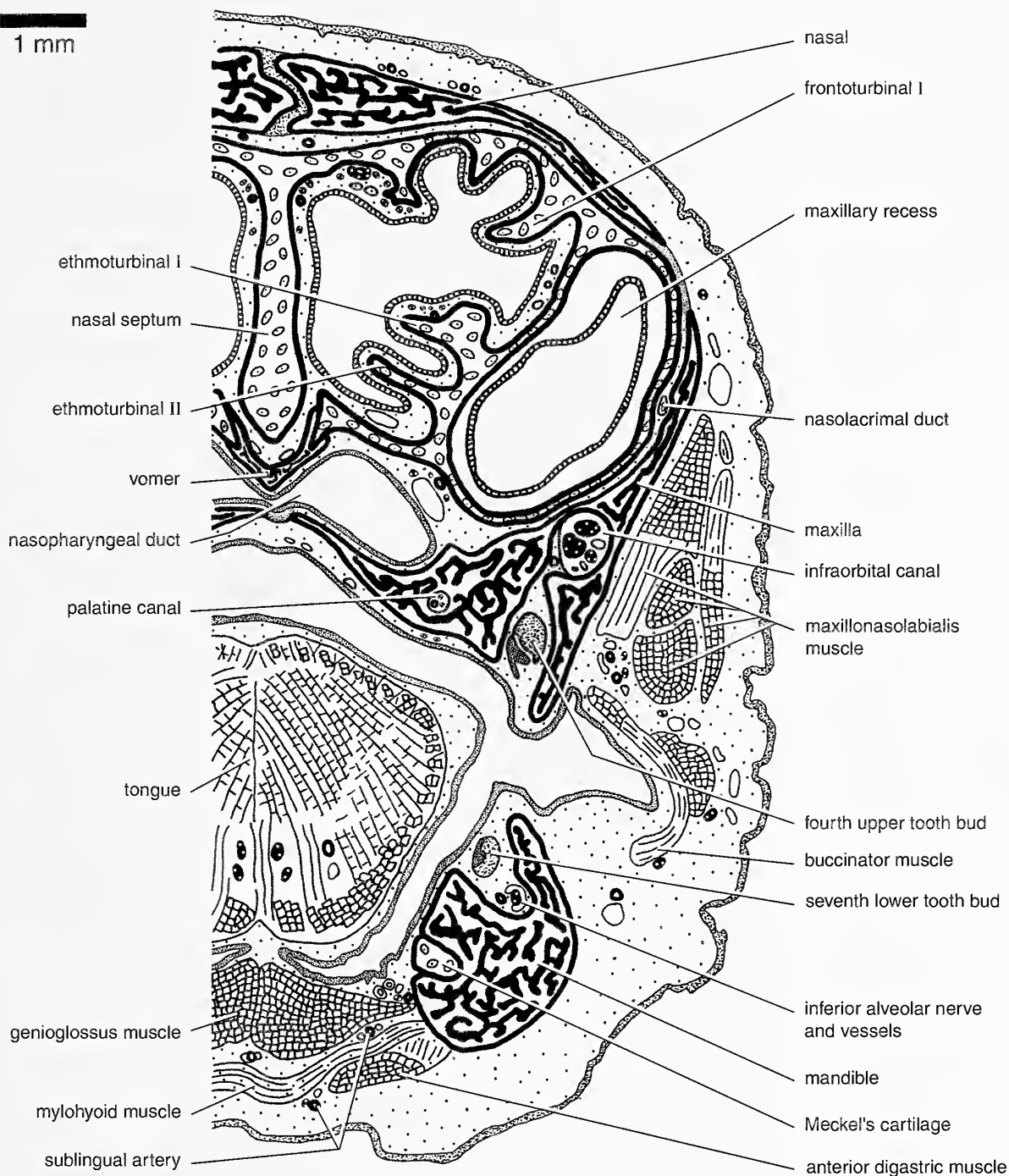


Fig. 13—*Euphractus sexcinctus* FMNH E28532, schematic representation of part of slide 699-1, a frontal section through the snout at the level of the infraorbital canal. The vomer ossification is invading the posterior part of the vomeronasal cartilages.

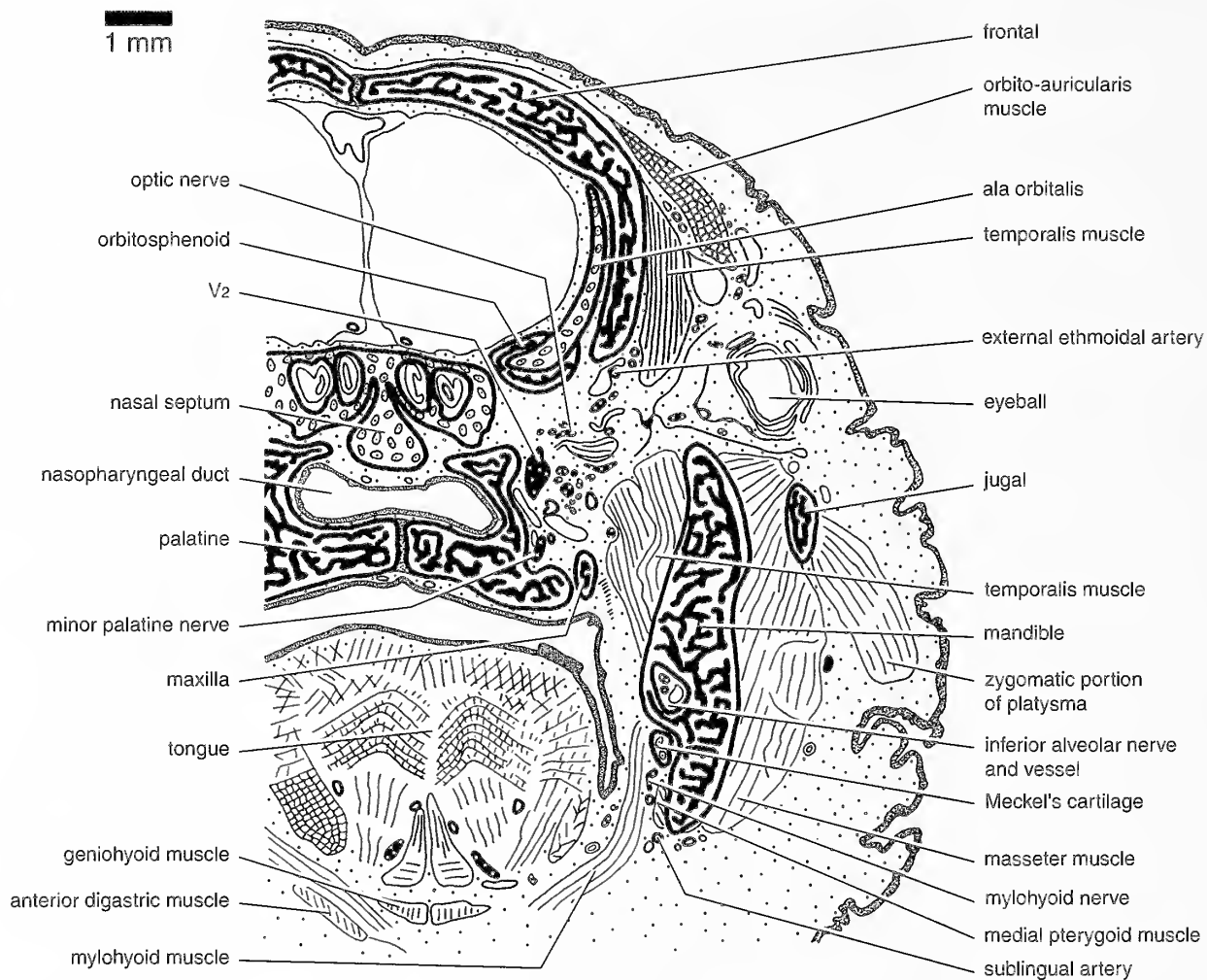


Fig. 14—*Euphractus sexcinctus* FMNH E28532, schematic representation of part of slide 550-2, a frontal section through the eyeball. The brain is damaged throughout the sectioned series and is not included in this or subsequent figures. The minor palatine nerve and vessels are entering a canal in the palatine.

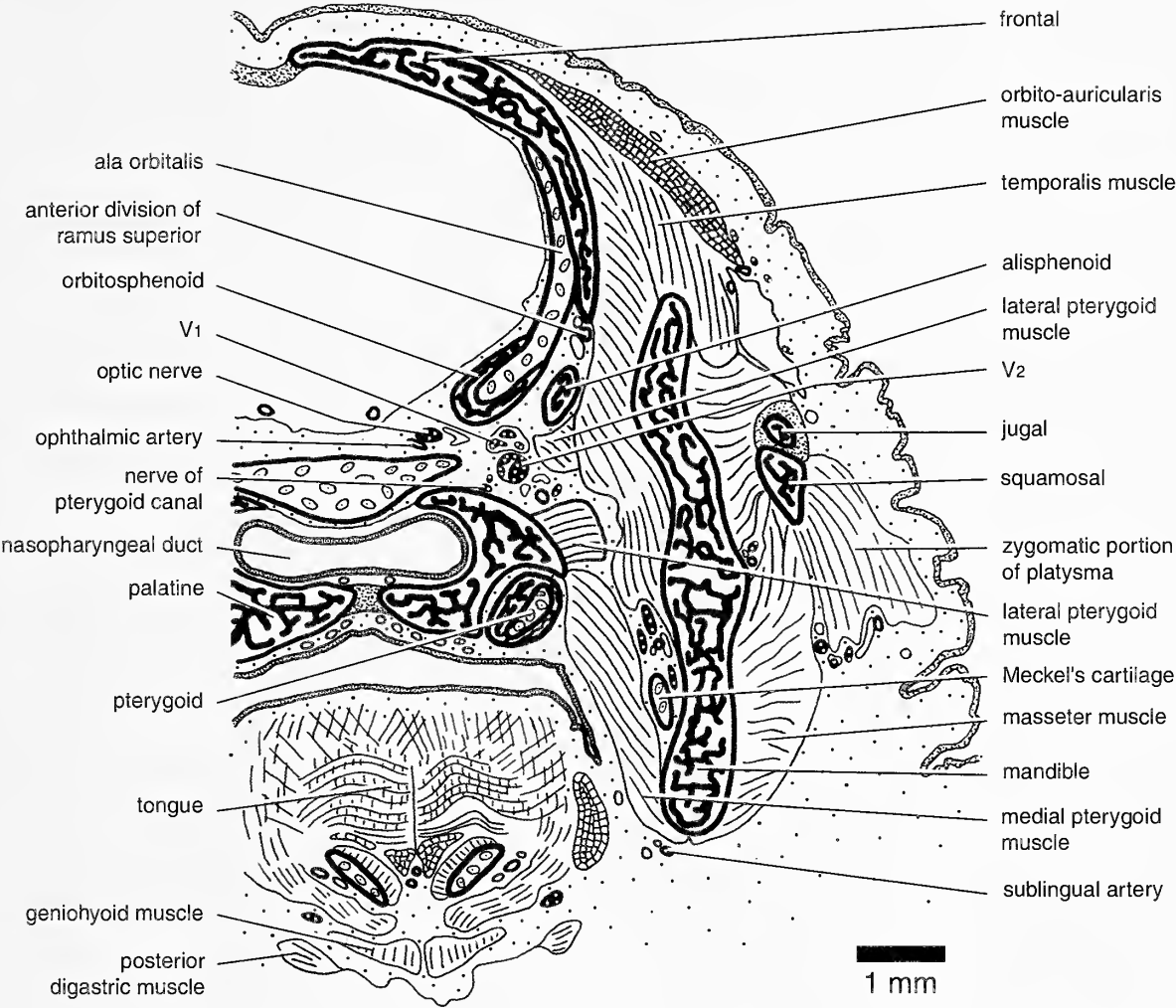


Fig. 15—*Euphractus sexcinctus* FMNH E28532, schematic representation of part of slide 514-2, a frontal section through the orbitotemporal region at the level of the optic canal and the anterior opening of the orbitotemporal canal. The pterygoid bone has intramembranous and cartilaginous components. Running in the gap between the medial pterygoid and temporalis muscles are the inferior alveolar nerve and vessels; the nerve of the pterygoid canal approaches the rostral opening of the pterygoid canal.

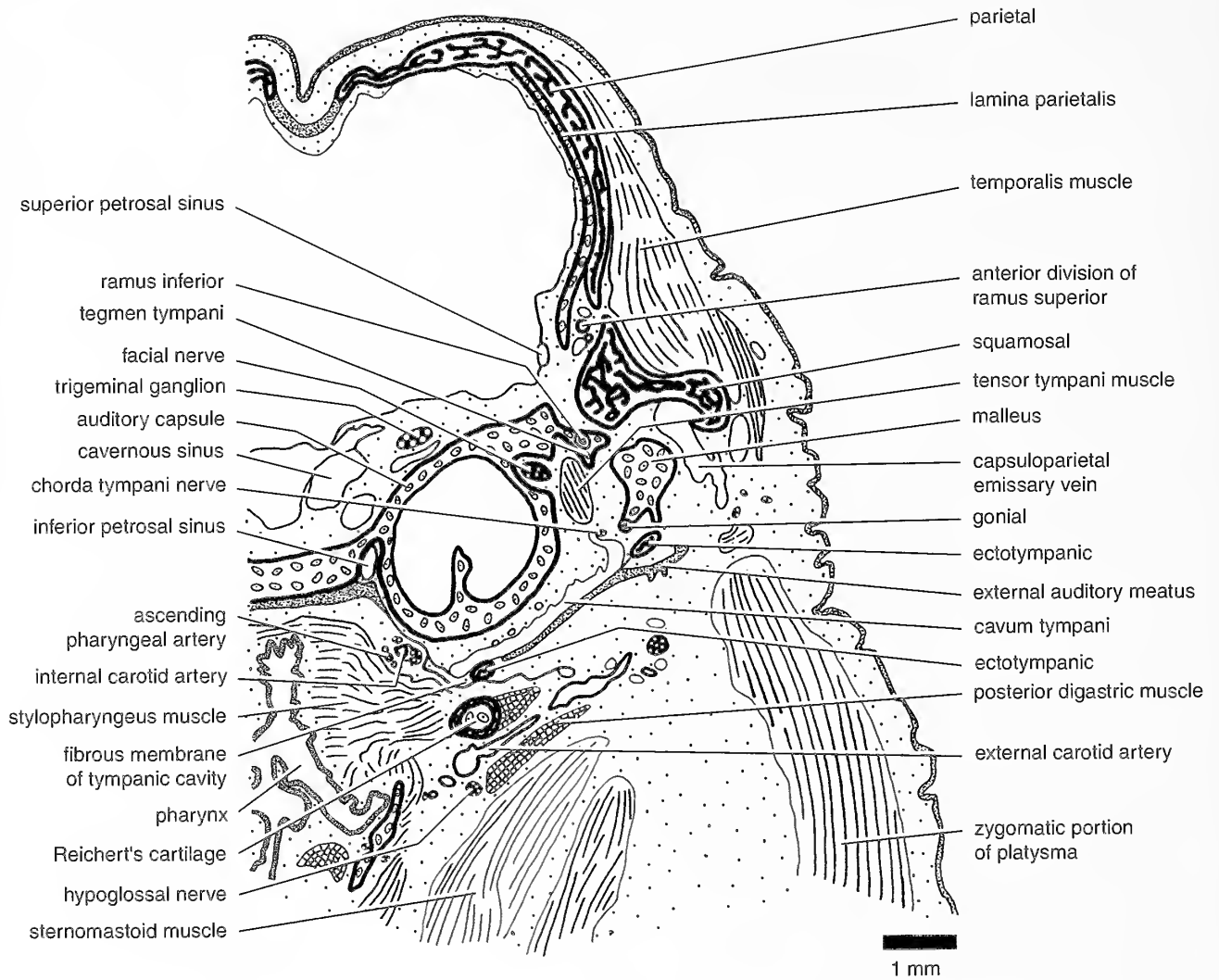


Fig. 16—*Euphractus sexcinctus* FMNH E28532, schematic representation of part of slide 399-1, a frontal section through the pars cochlearis of the auditory capsule. The orbitotemporal canal lies between the lamina parietalis, parietal, and squamosal; the capsuloparietal emissary vein exits the post-glenoid foramen; the ramus inferior (rostral tympanic artery) passes through the tegmen tympani; and the floor of the tympanic cavity consists of the ring-shaped ectotympanic bone and a fibrous membrane.

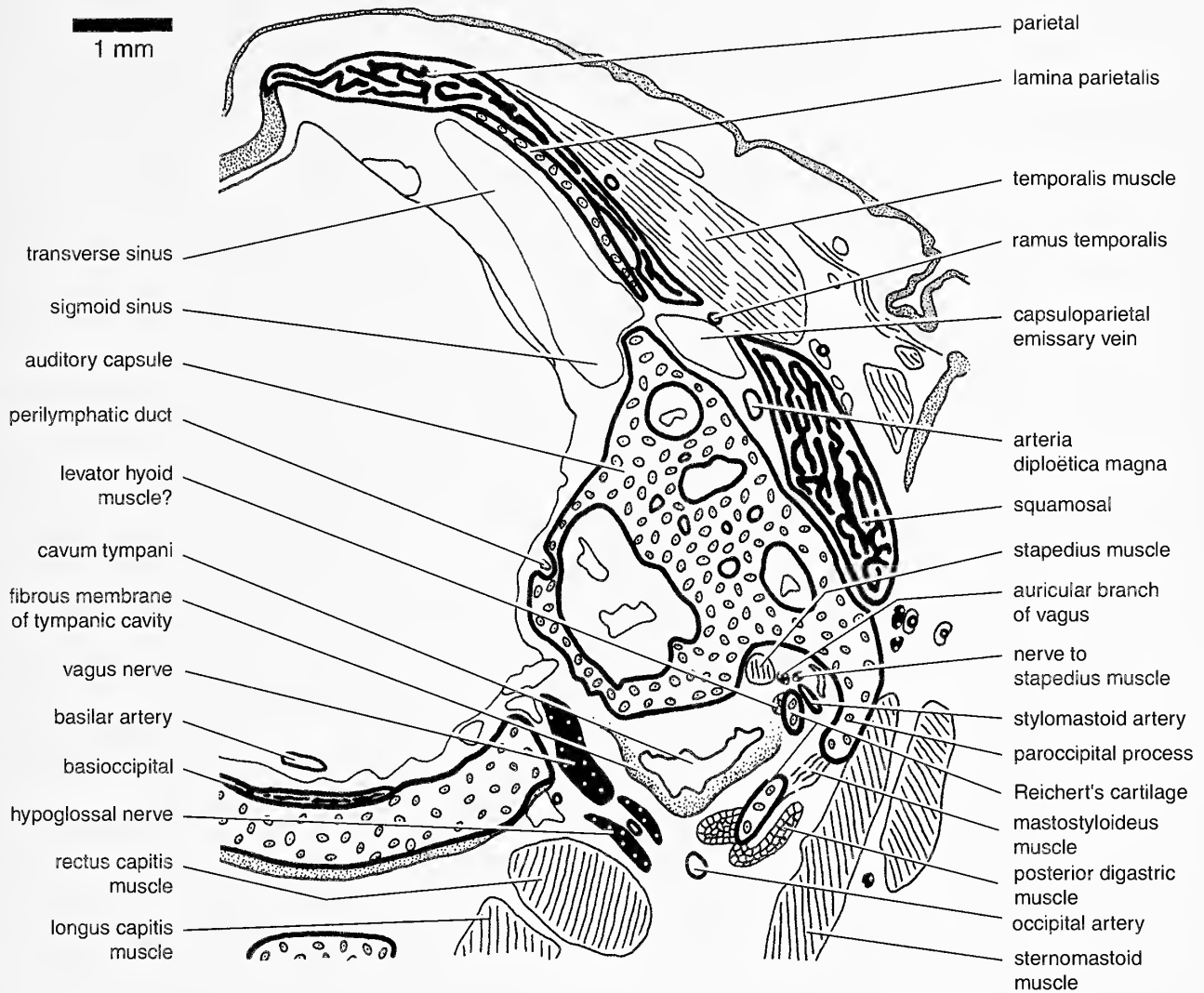


Fig. 17—*Euphractus sexcinctus* FMNH E28532, schematic representation of part of slide 321-2, a frontal section through the pars canalicularis of the auditory capsule. The posttemporal canal lies between the auditory capsule, lamina parietalis, parietal, and squamosal; the perilymphatic duct approaches the cochlear canaliculus; the jugular foramen lies between the auditory capsule and central stem; and the floor of the tympanic cavity consists of a fibrous membrane.

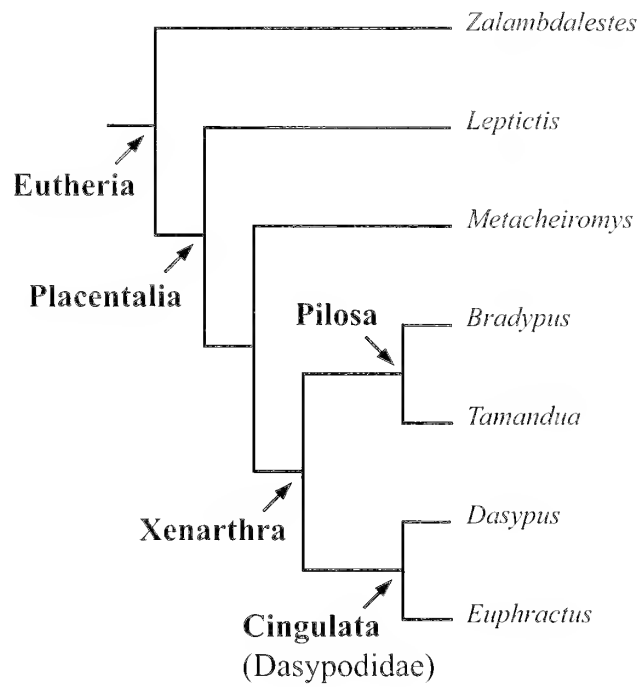


Fig. 18—Phylogenetic relationships of taxa employed in the comparative portion of this report. Relationships within Xenarthra are based on Delsuc et al. (2002, 2003) and Gaudin and Wible (in press). For the position of *Metacheiromys*, we follow Patterson et al. (1992), Gaudin (1995, 2004), and Szalay and Schrenk (1998), and for *Leptictis* and *Zalambdalestes*, we follow Wible et al. (2004).

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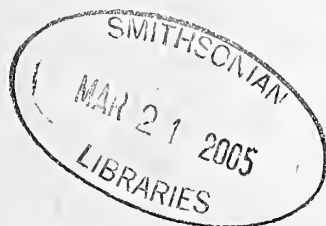
31 December 2004

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AMBEDUS PUSILLUS, NEW GENUS, NEW SPECIES, A SMALL DIADECTID
(TETRAPODA: DIADECTOMORPHA) FROM THE LOWER PERMIAN OF OHIO,
WITH A CONSIDERATION OF DIADECTOMORPH PHYLOGENY

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ABSTRACT

Ambedus pusillus, new genus, new species, is a small diadectid from the Lower Permian Greene Formation of Ohio that is distinguishable from all other members of the group by the presence of conical anterior teeth of the maxilla and dentary, high maxillary and mandibular tooth counts, a lesser degree of molarization of the cheek teeth, a shallow dentary, lack of a labial parapet, and a relatively shallow alveolar shelf that suggests a more shallow tooth implantation than that of other diadectids. The recognition of *A. pusillus* as a member of Diadectidae is supported by the presence of a heterodont dentition that possesses transversely expanded, molariform cheek teeth bearing: 1) a central cusp flanked by labial and lingual shoulders; and 2) wear facets developing on the lingual and labial shoulders of the maxillary and dentary cheek teeth, respectively. Although lacking a deep lower jaw, which is characteristic of herbivores and found in other diadectids, the presence of procumbent anterior teeth, molariform cheek teeth, and wear facets similar to those of other diadectids suggest that *Ambedus*, like all other diadectids, may have been herbivorous. Phylogenetic analysis of Diadectomorpha confirms its status as a natural group, and it supports both the monophyly of Diadectidae and the sister-group relationship of Diadectidae to *Tseajaia*. The recognition of *Limnoscelis* as the sister-taxon to *Tseajaia* + Diadectidae is also supported. Within Diadectidae, *Ambedus* is the sister-taxon to all other diadectids, with *Orobates*, *Desmatodon*, and *Diasparactus* + *Diadectes* representing progressively more derived taxa in a series of nested clades. With a greater species-richness and wider geographic range relative to other diadectomorph taxa, it is hypothesized that the evolution of herbivory in Diadectidae led to an evolutionary radiation of species within the group.

KEY WORDS: Diadectidae, *Ambedus*, Diadectomorpha, Tetrapoda, Greene Formation, Dunkard Group, Permian, herbivory

INTRODUCTION

The name Diadectidae was first proposed by Cope (1880a) to include the genera *Diadectes* and *Empedocles*, and within fifteen years of its description (Cope 1880b), nine additional genera were referred to the group. After significant taxonomic revisions (e.g., Case 1911; Olson 1947), six diadectid genera are currently recognized: *Phanerosaurus* Meyer, 1860; *Diadectes* Cope, 1878; *Stephanospondylus* (Geinitz and Deichmüller 1882); *Desmatodon* Case, 1908; *Diasparactus* Case, 1910; and *Orobates* Berman et al. 2004. *Desmatodon* is a Late Pennsylvanian taxon known primarily from skull material and dentition produced from the Missourian Red Knob Formation of Pennsylvania (Case 1908; Romer 1952; Berman and Sumida 1995), Missourian Sangre de Cristo Formation of Colorado (Vaughn 1969; Berman and Sumida 1995), and Virgilian Cutler Formation of New Mexico (Berman 1993). *Diasparactus* remains have been recovered from the Upper Pennsylvanian Virgilian Cutler and Ada formations of New Mexico and Oklahoma, respectively (Berman 1993; Kissel and Lehman 2002). The best known diadectid, *Diadectes*, is known from the Lower Permian of Colorado, New Mexico, Ohio, Oklahoma, Texas, Utah, West Virginia, Prince Edward Island, and Germany (Olson 1947; Langston 1963; Lewis and Vaughn 1965; Olson 1967; Berman 1971; Olson 1975; Berman 1993; Berman et al. 1998a), and *Phanerosaurus*, *Stephanospondylus*, and *Orobates* are

restricted to the Lower Permian of Germany (Berman et al. 1998a; Kissel et al. 2002; Berman et al. 2004). Reisz and Sutherland (2001) described a small collection of diadectid remains, including four frontals, one post-frontal, and 14 isolated teeth, that were collected from the Lower Permian near Richards Spur, Oklahoma. With the skull elements resembling those of *Diadectes absitus* and the dentition resembling that of *Orobates*, Reisz and Sutherland (2001) could not demonstrate that the Richards Spur diadectid elements are assignable to a single taxon, so a generic assignment of the material was considered premature, and the material remains unnamed.

Presented here is a new genus and species of Diadectidae from the Dunkard Group of Ohio. Collection data indicates that the specimens attributed to this new form, which was initially reported by Kissel and Reisz (2003), had been recovered from Clark Hill in Monroe County, Ohio, with the fossil-bearing horizon found approximately 8 feet (2.5 m) below the Nineveh Coal of the Greene Formation. The fossil remains are preserved in a light gray, micaceous claystone that weathers to tan. Remains of the dipnoan *Sagenodus*, the trimerorhachid *Trimerorhachis*, a possible embolomere, and the synapsid *Ctenospondylus ninevehensis* have also been reported from Clark Hill (Berman 1978). Produced from a single site in the Greene Formation, these four taxa were recovered from the Nineveh Limestone, which is interpreted as

a freshwater pond or lake deposit (Berman 1978). Recognition of the new form from Clark Hill marks only the second recorded occurrence of diadectid remains from Ohio and the third recorded occurrence of diadectid remains from the Dunkard. Olson (1970; 1975) reported the presence of *Diadectes* from the Belpre locality of Washington County, Ohio, and Berman (1971) referred a skull that was recovered from Roane County, West Virginia to *Diadectes*. With both the Belpre and Roane County localities found within the Washington Formation, the unit that underlies the Greene Formation, the new form represents the youngest diadectid recovered from the Dunkard. Age assignments of the Dunkard Group range from Late Pennsylvanian (e.g., Clendening 1975) to Early Permian (e.g., Durden 1975; Eagar 1975; Remy 1975), with the vertebrate taxa identified from Dunkard strata indicative of an Early Permian age (e.g., Berman and Berman 1975; Lund 1975; Olson 1975).

The purpose of this study is to describe this new genus and species of Diadectidae and examine its phylogenetic position within Diadectomorpha. When discussing characters of previously published phylogenetic analyses, the character numbers listed correspond to those assigned by the original authors.

INSTITUTIONAL ABBREVIATIONS

CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania

FMNH UC—Field Museum of Natural History, Chicago, Illinois

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

MNG—Museum der Natur, Gotha, Germany

OMNH—Sam Noble Oklahoma Museum of Natural History, Norman

UCMP—University of California Museum of Paleontology, Berkeley

YPM—Yale Peabody Museum, New Haven, Connecticut

SYSTEMATIC PALEONTOLOGY

Cotylosauria Cope, 1880a
 Diadectomorpha Watson, 1917
 Diadectidae Cope, 1880a
Ambedus, new genus

Diagnosis.—A small diadectid distinguishable from other members of the group by: 1) a shallow dentary; 2) rela-

tively high maxillary and mandibular tooth count; 3) lack of a labial parapet of dentary; 4) anterior teeth of maxilla and dentary conical, in contrast to the incisiform anterior teeth of other diadectids; and 5) shallow alveolar shelf, which suggests a relatively shallow tooth implantation.

Etymology.—Latin, *ambedo*, to nibble.

Ambedus pusillus, new species
 (Fig. 1–5)

Holotype.—MCZ 9436, nearly complete right maxilla.

Horizon.—Eight feet below Nineveh Coal Horizon, Greene Formation, Dunkard Group.

Locality.—Clark Hill, sec. 16, Salem Township, Monroe County, Ohio.

Diagnosis.—Same as that for the genus, this being the only known species.

Referred Specimens.—MCZ 9437, poorly preserved maxilla; MCZ 9438, complete left dentary; MCZ 9439, anterior portion of right dentary; MCZ 9440, posterior portion of left dentary; MCZ 9441, poorly preserved dentary.

Etymology.—Latin, *ambedo*, to nibble; *pusillus*, tiny.

DESCRIPTION AND COMPARISON

Introduction

The material assigned to *Ambedus pusillus* consists of two maxillae (MCZ 9436 and 9437) and four dentaries (MCZ 9438, 9439, 9440, and 9441) of varying completeness. Both MCZ 9437 and 9441 are poorly preserved, with much of the bone either missing or severely damaged, so the description of *A. pusillus* is restricted to four elements, a right maxilla (MCZ 9436) and a left (MCZ 9438) and two right (MCZ 9439 and 9440) dentaries. MCZ 9436 is incomplete anteriorly and also lacks the extreme posterior tip, and MCZ 9439 and 9440 lack the posterior and anterior portions, respectively. In order to preserve the impression of the sixth tooth of the series, matrix was not completely prepared from the anterior portion of MCZ 9439; thus, the anterior teeth of this specimen are exposed in lateral view only. MCZ 9438 is a complete left dentary exposed primarily in lateral view, with the occlusal surfaces of several teeth also exposed. Prior to their recognition as diadectid remains, the above specimens were collectively catalogued as MCZ 8667 and assigned to *Mycterosaurus* sp. Also referred to MCZ 8667 is an isolated humerus that was collected within the same vicinity as the maxillae and dentaries. Because the humerus exhibits no features indicative of Diadectidae, it

is not referred to *Ambedus pusillus*, and it is therefore not described herein.

Among diadectid taxa, the maxilla and dentary are known in *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*. The genus *Phanerosaurus* is based solely on an articulated series of four presacral and two sacral vertebrae (Meyer 1860), so comparison to it is not useful for this study. *Stephanospondylus* is known from a wider range of elements, including tooth-bearing elements of the upper and lower jaws (Stappenbeck 1905; Romer 1925), but it remains a poorly known taxon, and Berman et al. (1998a) suggest that the holotype may represent a juvenile form. Further evaluation of this taxon is required, and it is therefore not included in this study unless specifically noted. Thus, comparison of *A. pusillus* is restricted primarily to *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*, with comparison to the Richards Spur diadectid material restricted to dental morphology.

As discussed below, the remains described herein as *A. pusillus* possess none of the features that typify known juvenile individuals of previously described diadectid taxa. All elements are therefore thought to represent those of adult individuals.

Maxilla

The maxilla (Fig. 1) is represented by MCZ 9436, a nearly complete right maxilla that possesses 12 teeth and one empty alveolus. Only the extreme tip of the posterior end is lacking in MCZ 9436, but a larger portion of the anterior end is missing. Although the anterior portion of the tooth row is therefore likely incomplete in MCZ 9436, the preserved tooth positions are numbered from one to 13 for purposes of description, with tooth one representing the most anterior of the preserved teeth.

In lateral view, the dorsal margin is highly convex, as in the posterior region of the maxilla of both *Diadectes* and *Desmatodon*. The ventral margin is nearly horizontal, as in all diadectids. As preserved, the lateral surface is rough and pitted, but this texture no doubt results from poor preservation and crushing of the lateral surface, especially of the very thin dorsal lamina. With the exception of small foramina just above the tooth row, the lateral surface was likely smooth, as in the dentary, and it is flat and vertical. The dorsal portion of the dorsal lamina is displaced medially relative to the ventral portion of the lateral surface, but this displacement results from movement along a postmortem break that extends anteriorly from the posterior margin of the dorsal lamina to the level of the fifth tooth.

Description of the medial surface of the maxilla is restricted to the alveolar shelf, as the thin, fragile nature of the dorsal lamina prevented its complete preparation. The alveolar shelf is smoothly finished and, relative to other diadectids, shallow. It is a convex, rounded ridge to

the level of the fifth tooth. At the sixth tooth position, an arcuate groove originates from the ventral margin and extends to the ventral margin at the level of tooth ten. Anteriorly, the groove is wide and faces medially, but as it extends dorsoposteriorly, it narrows and faces dorsally and slightly medially. Posteriorly, the groove widens to form a dorsomedially facing platform. A ridge defines the dorsal margin of the groove anteriorly. Ventral to the groove, the alveolar shelf is convex. From the level of tooth five to tooth seven, the dorsal surface of the alveolar shelf is a flat, dorsally facing platform. It is slightly convex and faces dorsomedially throughout its remaining length.

MCZ 9436 possesses 13 teeth, including the empty alveolus at tooth position four. Because the anterior portion of MCZ 9436 is lacking, it can only be stated that a minimum of 13 maxillary teeth were present. In MCZ 9436, tooth 13 likely represents the last tooth of the maxillary series, so only the anteriormost maxillary teeth are not preserved. Maxillary tooth counts in other diadectids include 11 for *Diadectes* (Case and Williston 1912; Berman et al. 1998a), 12 for *Desmatodon* (Berman and Sumida 1995), 12 for *Orobates* (Berman et al. 2004), and the right maxilla of *Stephanospondylus* illustrated by Geinitz and Deichmüller (1882, plate IV, fig. 2) possesses a series of 12 teeth (Romer 1925).

The shallow alveolar shelf in *Ambedus pusillus* suggests that tooth implantation was not as deep as that in other diadectids. Whereas the root is longer than the height of the crown in *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*, the shallow alveolar shelf of MCZ 9436 indicates that root length is less than crown height in *Ambedus*, as observed in the diadectomorphs *Limnoscelis* and *Tseajaja*. In no specimen is it possible to determine if the marginal teeth of *Ambedus* exhibit infolding of the dentine, a feature present in all other diadectomorphs.

In occlusal view, the maxillary dentition is aligned in a straight row with only a slight lateral deflection anteriorly. It is possible that, if the tooth row were completely preserved, this deflection would continue and become more prominent, as in other diadectids. The maxillary dentition of heretofore known diadectids consists of two incisiform teeth that are succeeded by a series of molari-form cheek teeth. The incisiform teeth are oval in section near the base and are excavated lingually on the distal half to produce a chisel-like distal tip, and the cheek teeth are transversely expanded with an occlusal surface that possesses a central cusp flanked by labial and lingual shoulders. The maxillary dentition of *Ambedus* adheres to this general pattern, but the anteriormost teeth of MCZ 9436 are not incisiform. Since the anterior portion is lacking in MCZ 9436, it is likely that the anterior teeth of the maxilla are also not preserved, opening the possibility that the anterior teeth, if present, would exhibit an incisiform morphology. However, the lack of incisiform anteri-

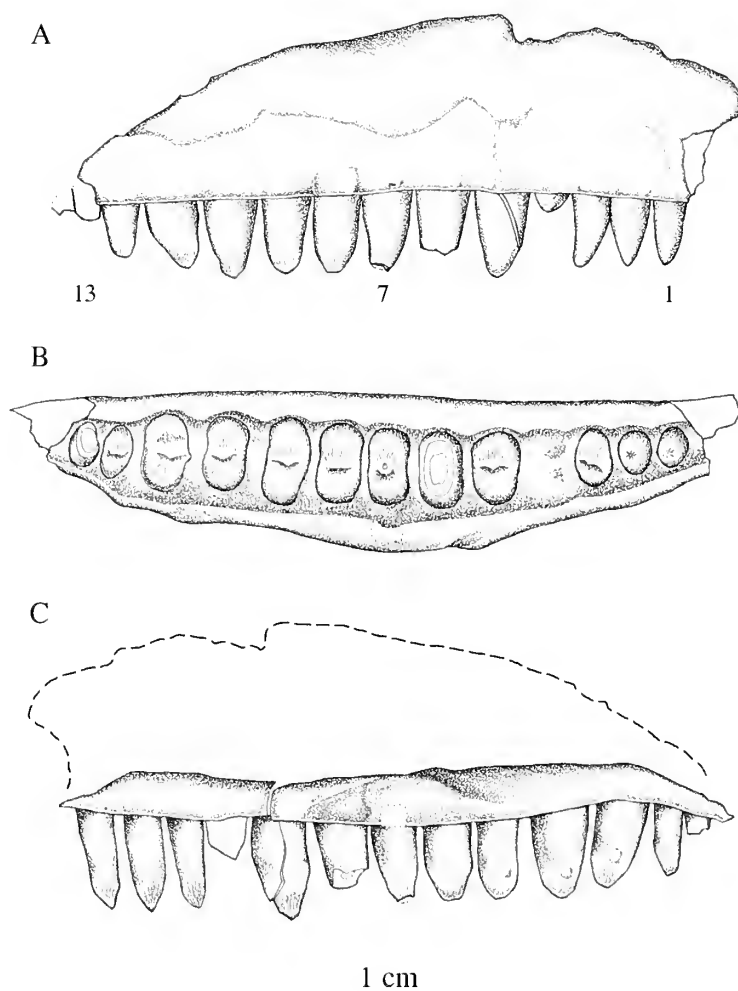


Fig. 1.—MCZ 9436, right maxilla and holotype of *Ambedus pusillus* in lateral (A), occlusal (B), and medial (C) views. Numbers indicate tooth positions.

or teeth on the dentary, as described below, strongly suggests that the upper tooth row also lacked incisiform dentition. As the tooth row in MCZ 9436 extends posteriorly, the teeth gradually expand transversely until tooth position nine, from which point they decrease in transverse width posteriorly to the end of the series. The alveolar shelf attains its greatest mediolateral width at the level of tooth seven in order to accommodate the transversely expanded cheek teeth. In *Diadectes*, the maxillary cheek teeth increase in width to the sixth or seventh tooth and then decrease to the posterior end of the series (Case and Williston 1912; Berman et al. 1998a). A similar pattern is found in CM 47654, a left maxilla of *Desmatodon hesperis*, but the serial decrease in width after the widest tooth, tooth seven, is less drastic than that in *Diadectes*.

The first two teeth of the maxillary series of *Ambedus pusillus* are conical with a weakly developed lingual shoulder and a medially directed central cusp.

Tooth three is the first of the series to exhibit the transversely expanded, molariform cheek teeth that are characteristic of diadectids, although the labial shoulder is weakly developed and the central cusp possesses a slight medial tilt. On teeth one to three, longitudinal fluting is present on the distal third of the lingual surface. Tooth four is not preserved. The fifth tooth possesses both labial and lingual shoulders, but the lingual shoulder is the larger of the two. Also, beginning with tooth five and present on the remaining teeth of the series, the central cusp is directed dorsally and longitudinal fluting is present on the distal half of the lingual surface and near the tip on the labial surface. Although tooth four is not present and tooth six is incomplete, they were likely intermediate in form between teeth three and five and five and seven, respectively.

Teeth seven to 11 possess a uniform morphology, with a low central cusp flanked by rounded shoulders

both labially and lingually, lacking the prominent labial and lingual cusps found in the cheek teeth of *Diasparactus* and all species of *Diadectes* except *D. absitus*. In *D. absitus*, the maxillary cheek teeth each bear a tall central cusp, and the labial and lingual cusps are poorly developed, resembling shoulders more than cusps (Berman et al. 1998a). The cheek teeth of *Desmatodon* possess well-developed central and lingual cusps, with a rounded shoulder labially.

With a nearly vertical labial surface and a medially sloping lingual surface near the base of the crown, the outline of the cheek teeth in posterior view (Fig. 2A) differs considerably from other diadectids. In *Orobates* and the unnamed Richards Spur diadectid, the cheek teeth exhibit an exaggerated teardrop, or spade-like, outline (Reisz and Sutherland 2001; Kissel et al. 2002), and *Diadectes*, *Diasparactus*, and *Desmatodon* exhibit abrupt, shoulder-like expansion of the labial and lingual margins dorsal to a slight constriction between the crown and root. Tooth nine of MCZ 9436 possesses the greatest transverse width of the series, and it also exhibits the greatest degree of molarization of the series. Berman and Sumida (1995) demonstrated that the cheek teeth in adult specimens of *Diadectes* possess a greater degree of molarization than those of adult *Desmatodon* specimens (i.e., the cheek teeth of *Diadectes* have a much greater transverse width relative to their anteroposterior length and dorsoventral height than those of *Desmatodon*). *Ambedus* possesses a similar degree of molarization as *Desmatodon hesperis* and a significantly lesser degree of molarization than both *Diadectes lentus* and *Desmatodon hollandi* (Table 1), with the similar height/width ratios exhibited by *A. pusillus* and *D. hesperis* resulting from the tall, well-developed central cusp of the latter species, in contrast to the low central cusp of the former, and not from a similarity in tooth morphology. Tooth 12 possesses a lesser degree of molarization than those teeth anterior to it, its morphology resembling tooth three. Only the base of tooth 13 is preserved, and it possesses a subcircular section.

Wear facets are present on the lingual shoulders of teeth nine, 10, and 11 in MCZ 9436. Such an uneven wear pattern of the maxillary cheek teeth, with a greater degree of wear on the lingual shoulder or cusp than on the labial shoulder or cusp, is characteristic of diadectids (Berman et al. 1998b). Of these wear facets, none possess microwear patterns (e.g., striations) that may indicate a direction, or directions, of jaw movement during oral processing.

Dentary

The dentary (Figs. 3, 4, 5) is long and shallow, in strong contrast to that of all other diadectids in which the element is known. In *Diadectes* (Welles 1941; Berman et al. 1998a), *Desmatodon* (Berman and Sumida 1995),

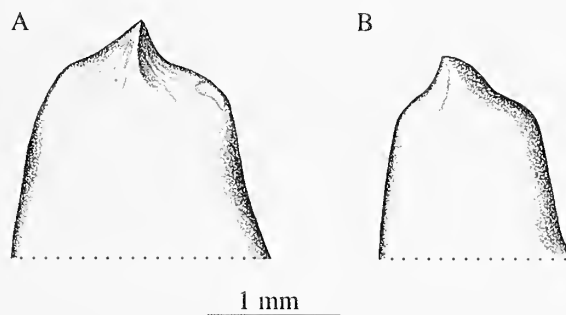


Fig. 2.—Fifth posteriormost maxillary tooth of MCZ 9436 (A) and fifth posteriormost dentary tooth of MCZ 9440 (B) in posterior view.

Stephanospondylus (Romer 1925), and likely *Diasparactus*, it is relatively short anteroposteriorly and deep dorsoventrally. The complete mandible of *Diasparactus* is known, but sutures delineating the individual elements are not visible (Case and Williston 1913); however, with the general morphology of the mandible and the known morphology of the dentary resembling that of *Diadectes* (Case and Williston 1913; Kissel and Lehman 2002), it is probable that the complete dentary of *Diasparactus* was similar to that of *Diadectes*.

Along the tooth-bearing area, the dorsal margin of the dentary of *Ambedus* is only slightly concave in lateral view. Posterior to the last tooth of the series, the margin is gently convex. In lateral view, the ventral margin is convex anteriorly and concave posteriorly. The ventral margin slopes posteroventrally, with the dentary possessing the greatest dorsoventral height posteriorly. In dorsal view, the dentary is thin anteriorly, expanding posteriorly to attain its greatest mediolateral width at tooth positions 14 and 15.

With the exception of several foramina and shallow, longitudinal grooves found below the tooth row, the lateral surface is smooth. In other diadectids, the lateral surface of the dentary is irregularly sculptured with prominent grooves and pits. Below the tooth row, the lateral surface, which is vertical in other diadectids, curves and continues as a flat surface that extends ventromedially, undercutting the alveolar shelf so that the ventral margin of the dentary lies medial to the tooth row in anterior view. The dentary lacks the labial parapet and associated groove that is found in *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*. Although initially described by Berman et al. (1998a) as lacking a labial parapet, further preparation of the holotype of *Diadectes absitus* (MNG 8853) has revealed the presence of a low parapet (D. S. Berman, pers. comm.). In the paratype of *D. absitus* (MNG 8747), the right mandible is incompletely preserved, making determination of the presence of a labial parapet impossible, but it does possess a flat, dorsally facing platform lateral to the tooth row posteriorly (Berman

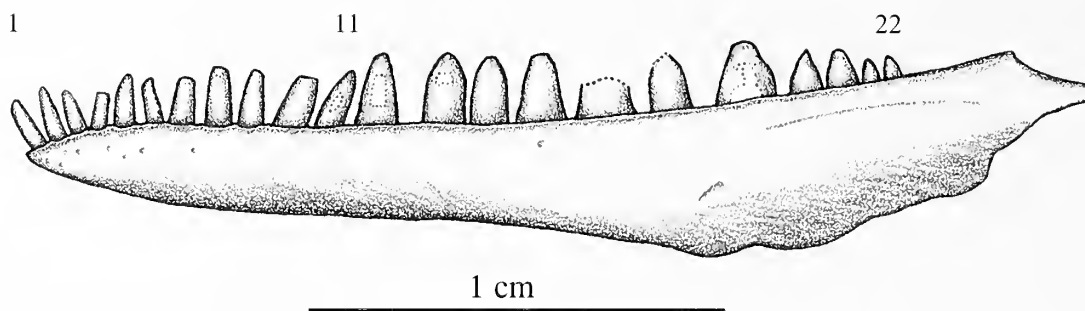


Fig. 3.—MCZ 9438, complete left dentary of *Ambedus pusillus* in lateral view. Numbers indicate tooth positions.

et al. 1998a), a feature also not present in *Ambedus*.

The medial surface of the dentary is traversed by a deep meckelian canal along its length. Anteriorly, the symphysis occupies the entire tip of the medial surface, extending posteriorly to the level of the third tooth. Its surface is rough and therefore distinct from the remaining medial surface. The meckelian canal continues anteriorly to divide the symphysis into distinct dorsal and ventral areas, leaving only a small area at the anterior tip of the symphysis to connect these two surfaces. The canal is shallowest within the symphysis, deepening and expanding dorsoventrally as it extends posteriorly. Dorsal to the canal, the medial surface of the dentary is convex from the symphysis to the level of the eighth tooth. Posterior to that position, the medial surface is flat and oriented vertically. Aside from a series of mostly longitudinal grooves found posterior to tooth position 12, the medial surface dorsal to the canal is smooth. Ventral to the canal and posterior to the symphysis, the medial surface is flat and smoothly finished to the level of the thirteenth tooth position, and it is inclined slightly so that the ventral margin lies slightly lateral to the dorsal margin. At the level of the thirteenth to fourteenth tooth position, the meckelian canal expands to completely excavate the ventral half of the medial surface of the dentary posteriorly. Thus, whereas its dorsal border is well-defined by the medial surface of the dentary throughout its entire length dorsally, the canal is well-defined ventrally from the symphysis to the level of tooth 13. As in the maxilla, the alveolar shelf is shallow relative to that of other diadectids, suggesting a relatively shallow tooth implantation in the dentary.

MCZ 9438, a complete left dentary, possesses a complete tooth row, and a total of 22 teeth are present. Incomplete posteriorly, MCZ 9439 possesses the first 18 teeth of the mandibular series, and MCZ 9440 is incomplete anteriorly, possessing teeth six to 22. Such a tooth count represents the greatest yet recorded for a diadectid, with the mandibular tooth counts of other diadectids including 14 to 18 for *Diadectes* (Case 1911; Case and Williston 1912; Welles 1941; Berman et al. 1998a), 15 for

Diasparactus (Kissel and Lehman 2002), 14 for *Desmatodon* (Berman and Sumida 1995), 17 for *Orobates* (Berman et al. 2004), and possibly 15 for *Stephanospondylus* (Romer 1925).

MCZ 9438, MCZ 9439, and MCZ 9440 all possess a similar dental morphology. In dorsal view, the dentition is aligned in the sigmoid curvature common to diadectids, but this curvature is slight and not as pronounced as in other members of the group. As in the upper jaw, the mandibular dentition of diadectids is differentiated into incisiform anterior teeth, molariform cheek teeth, and a short series of teeth intermediate to these two forms. However, whereas the anterior dentary teeth of other diadectids are strongly incisiform, those of *Ambedus pusillus* are conical; they are round in section near the base and terminate in a point, lacking the chisel-shaped, incisiform character of all other diadectids. As in other diadectids, however, the anterior dentary teeth are procumbent. Tooth 12 is the first transversely expanded tooth of the series, with teeth nine to 11 intermediate to the pointed anterior teeth and the expanded cheek teeth. The cheek teeth of the dentary possess a lesser degree of molarization than those of the maxilla (Fig. 2; Tables 1, 2) and a significantly lesser degree than the dentary cheek teeth of *Diadectes lentus*, *Diasparactus zenos*, and *Desmatodon hesperis* (Table 2). As exhibited by MCZ 9438, 9439, and 9440, they possess a low central cusp flanked by rounded shoulders both labially and lingually, not unlike those of the maxilla. In posterior view, both the labial and lingual surfaces are nearly vertical, although the lingual surface slopes medially near the base of the teeth (Fig. 2B). The teeth increase in size serially to tooth 18, from which point they slightly decrease in size posteriorly.

Nearly all of the dentary teeth possess wear surfaces, with the tips of the anterior conical teeth and the central cusp of the cheek teeth exhibiting wear. In MCZ 9439, teeth 13 to 18 are heavily worn, reducing the occlusal surfaces to smooth, flat surfaces that face dorso-medially. A smaller wear facet is present on the labial shoulder of tooth 16 in MCZ 9440. What may represent

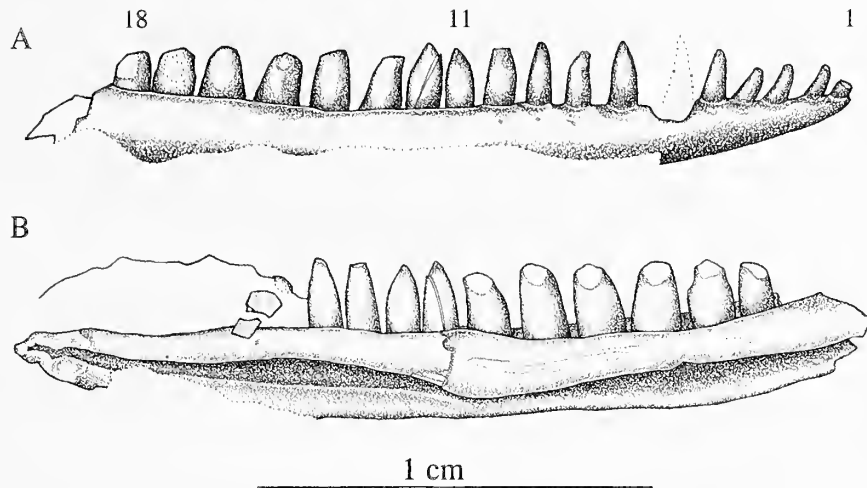


Fig. 4.—MCZ 9439, right dentary of *Ambedus pusillus* in lateral (A) and medial (B) views. Numbers indicate tooth positions.

wear facets are present on the labial shoulders of teeth 17, 18, and 21 in MCZ 9440, but these “facets” may just represent damage to the surface of the teeth. The wear pattern exhibited on teeth 13 to 18 of MCZ 9439 and tooth 16 of MCZ 9440, with a greater degree of wear on the labial cusp or shoulder of the dentary cheek teeth, is characteristic of diadectids (Berman et al. 1998b). As in the maxillary dentition, none of these wear facets possess microwear patterns that may facilitate the reconstruction of jaw movement during oral processing.

DISCUSSION

Ambedus pusillus and diadectid ontogeny

The small size of the maxilla and dentaries described herein as *Ambedus pusillus* invites the hypothesis that these elements are simply the remains of a juvenile individual of a previously described diadectid taxon, but such an interpretation is refuted by the following observations. A maxilla (CM 47668) identified as a juvenile form of *Desmatodon hesperis* possesses four dental features that are absent or greatly reduced in mature specimens of the genus and not present in specimens of *Diadectes* of any age: 1) fewer number of teeth; 2) greater relative spacing between teeth to produce large gaps between teeth; 3) first two maxillary teeth relatively longer and more incisiform; and 4) absence of wear facets (Vaughn 1972; Berman and Sumida 1995). The maxillary teeth of *Ambedus*, in contrast, outnumber those of adult *Desmatodon hesperis* specimens, they are packed tightly with little space between them, and they possess wear facets. In juvenile specimens of *Diadectes*, the cheek teeth exhibit a lesser degree of molarization than seen in the adult forms, with little or no transverse widening, a

weakly developed central cusp, and no labial or lingual cusps (Berman and Sumida 1995). Immature individuals of *Diadectes* do, however, possess a labial parapet (Berman et al. 1998a), a feature not present in *Ambedus*. Furthermore, the conical anterior dentary teeth of *A. pusillus* are distinctly different than those of *Diadectes* and *Desmatodon*, which do not exhibit any changes in their incisiform morphology throughout ontogeny (Berman and Sumida 1995).

With the understanding of diadectid ontogeny currently limited to studies of *Diadectes* and *Desmatodon* by Vaughn (1972) and Berman and Sumida (1995), comparison to immature individuals of the remaining diadectid taxa is not possible. However, in no known juvenile or adult of any diadectid taxon is the dentary as long and shallow as it is in *Ambedus*, supporting the conclusion that the material described as *Ambedus* does not represent the juvenile remains of a currently known diadectid, but rather represents a unique member of the group.

Phylogeny of Diadectomorpha

Heaton (1980) proposed that Diadectomorpha represents a monophyletic group that consists of (Limnoscelidae (Tseajaiidae + Diadectidae)). Subsequent studies (e.g., Gauthier et al. 1988; Laurin and Reisz 1995, 1997, 1999; Lee and Spencer 1997) indicated that Diadectomorpha is the sister-taxon to Amniota, with Diadectomorpha + Amniota constituting Cotylosauria. However, in none of these analyses is *Tseajaia* incorporated, leaving Diadectomorpha as a monophyletic group consisting of *Limnoscelis* and diadectids. The only study since that of Heaton (1980) to consider the interrelationships of diadectomorphs is that of Berman et al. (1992). Based on a data matrix of seven taxa and nine characters of the tem-

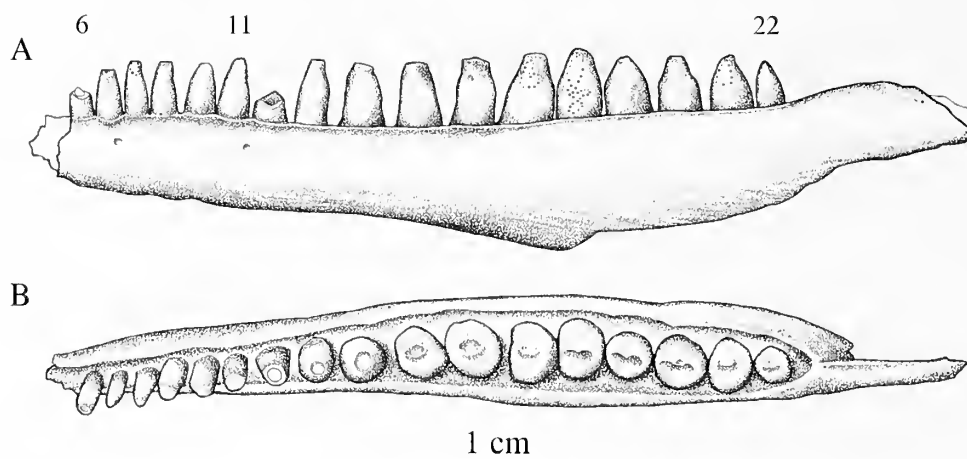


Fig. 5.—MCZ 9440, left dentary of *Ambedus pusillus* in lateral (A) and occlusal (B) views. Numbers indicate tooth positions.

poral and occipital region, the analysis of Berman et al. (1992) supported the conclusions of Heaton (1980), with Diadectomorpha consisting of (*Limnoscelis* (*Tseajaia* + *Diadectes*)).

In order to evaluate the phylogenetic position of *Ambedus pusillus*, a new phylogenetic analysis of Diadectomorpha is presented here. It includes nine taxa, including two outgroups, and 37 cranial, dental, and post-cranial characters (Appendix 1, 2). Because it is incompletely known, *A. pusillus* is scored for only seven of these 37 characters; however, following the conclusions of Kearney and Clark (2003), *A. pusillus* is included in the analysis despite its incomplete nature. The analysis incorporates a number of characters that are derived from the analyses of Gauthier et al. (1988), Berman et al. (1992), Laurin and Reisz (1995, 1997), Lee and Spencer (1997), Berman et al. (1998a), and Berman (2000), but only characters that were found by these authors to possess an unambiguous history were incorporated into the current analysis. Laurin and Reisz (1997) regarded the absence of a tabular-parietal contact [24(0)] and the presence of uncinat processes [123(1)] as autapomorphies of *Diadectes*, but no specimens of *Diadectes* examined for this study possess uncinat processes, and the tabular does contact the parietal in *Diadectes*, as indicated by Berman et al. (1998a) and Berman (2000), and all diadectomorphs in which that region of the skull is known. Thus, since characters 24(0) and 123(1) of Laurin and Reisz (1997) do not represent autapomorphies of *Diadectes*, they are not included here.

Outgroups in the present analysis include Amniota, the sister-group to Diadectomorpha, and Lepospondyli. Although *Solenodonsaurus* has been found to be the sister-group to Cotylosauria (Gauthier et al. 1988; Laurin and Reisz 1999), the specimens referred to that genus are

fragmentary and lack much anatomical information; thus, Lepospondyli, the sister-taxon to *Solenodonsaurus* + Cotylosauria, was selected as the second outgroup. Within Diadectomorpha, *Limnoscelis*, *Tseajaia*, *Ambedus*, *Orobates*, *Desmatodon*, *Diasparactus*, and *Diadectes* were analyzed. Due to their incomplete nature and uncertain affinities, *Phanerosaurus*, *Stephanospondylus*, and the Richards Spur diadectid(s) were not included in the analysis. Since *Tseajaia* remains the only genus assigned to Tseajaiidae, and all limnoscelids have been referred to the genus *Limnoscelis* (Wideman 2002), both Tseajaiidae and Limnoscelidae represent monogeneric taxa, so the nomina Limnoscelidae and Tseajaiidae are therefore abandoned.

Using Paup 4.0b10 (branch and bound search; Swofford 2002) and MacClade 4.0 (Maddison and Maddison 2000), the analysis yielded a single most parsimonious tree with a length of 53 steps, a consistency index (CI) of 0.8491, and a retention index (RI) of 0.8261. The resulting tree (Fig. 6) supports the previous hypothesis that *Limnoscelis*, *Tseajaia*, and diadectids form a monophyletic group, with diadectids and *Tseajaia* sharing a more recent common ancestor than either does with *Limnoscelis*. The monophyly of Diadectidae is also supported, with diadectids consisting of a series of nested clades that terminates with *Diasparactus* + *Diadectes*. Diadectidae is defined here as *Diadectes* and all taxa sharing a more recent common ancestor with *Diadectes* than with *Tseajaia*.

Ambedus is found to be the sister-taxon to all other members of Diadectidae. Although the known remains of *Ambedus* lack many of the structures considered in the analysis, the absence of a labial parapet of the dentary, deep tooth implantation, deep lower jaw, and well-developed molariform teeth with lateral and lingual cusps

supports the position of *Ambedus* as the sister-taxon to all other diadectids.

Node E is diagnosed by the presence of a labial parapet of the dentary [22(1)], the presence of marginal teeth with roots longer than the height of the crown [26(2)], and the presence of incisiform anterior teeth [28(1)]; node F is diagnosed by the presence of a secondary palatal shelf [12(1)] and the presence of a deep lower jaw [20(1)]; and node G is diagnosed by the presence of a jaw articulation located ventral the occlusal plane [19(1)], the presence of a tall labial parapet [22(2)], the presence of a high degree of molarization of the cheek teeth [30(2)], and the presence of well-developed labial and lingual cusps of the cheek teeth [31(2)]. Thus, the phylogeny of Diadectidae presented here suggests that a trend toward more efficient oral processing characterizes the evolutionary history of the group. The labial parapet of the dentary may have supported a beak (Welles 1941), served as a masticatory surface for the labial margins of the maxillary cheek teeth (Berman et al. 1998b), or both; the secondary palatal shelf may have provided an occlusal surface for the dentary cheek teeth (Olson 1947; Berman et al. 1998b); and a massive lower jaw, the depression of the jaw joint relative to the occlusal plane, and transversely expanded cheek teeth are three skeletal features indicative of herbivory (Olson et al. 1991; Hotton et al. 1997; Sues and Reisz 1998; Reisz and Sues 2000).

As previously stated, the analyses of Gauthier et al. (1988), Laurin and Reisz (1995, 1997, 1999), and Lee and Spencer (1997) hypothesized that Amniota and Diadectomorpha are sister-taxa. Berman et al. (1992) and Berman (2000) concluded differently, suggesting that Synapsida is the sister-taxon to Diadectomorpha. This latter hypothesis, due to its unconventional nature, deserves consideration here. Berman et al. (1992) united synapsids and diadectomorphs based on the presence of three synapomorphies: 2(1), posterolateral corner of the skull table formed entirely or nearly entirely by the supratemporal; 3(1), long posterior expansion of postorbital contacts supratemporal to exclude the parietal lappet from contacting the squamosal; and 5(1), possession of an otic trough. These characters are problematic. Although character state 2(1) is present in early synapsids, recently described remains of *Diadectes* indicate that the posterolateral corner of the skull table of *Diadectes* is formed subequally by the supratemporal and tabular (Berman et al. 1998a), a condition shared with all other diadectids in which this region of the skull is known, *Desmatodon* (Vaughn 1972; fig. 4) and *Orobates* (Berman et al. 2004). As evidenced by YPM 811, the holotype of *Limnoscelis paludis*, the type species of the genus, the posterolateral corner of the skull table of *Limnoscelis* is also characterized by near equal contributions of the supratemporal and tabular. Only in *Tseajaia* does the tabular only contribute slightly to the posterolateral corner of the skull table, with

the supratemporal representing the dominant element of the region (Moss 1972). Thus, the presence of a skull table in which the posterolateral corner is formed entirely or nearly entirely by the supratemporal [7(1) of the present study] is not shared by synapsids and all diadectomorphs, and its presence in *Tseajaia* and synapsids may represent a convergence. As indicated by Laurin and Reisz (1995), the second character [3(1)] of Berman et al. (1992) is present in diadectomorphs and all of Amniota, whereas the third [5(1)] may have evolved convergently in both diadectomorphs and Synapsida, since several early synapsids (e.g., *Eothyris*, *Varanops*, and *Aerosaurus*) have no otic trough.

Based on an analysis of eight characters of the occipital region, Berman (2000) cited the following three synapomorphies to link diadectomorphs and synapsids: 5(2), a deep, nonsculptured component of the tabular contacts the distal end of a ventrally displaced, laterally directed paroccipital process, enclosing laterally a small, ventrally displaced, posttemporal fenestra; 6(1), presence of an otic trough of the opisthotic; and 7(1), posterolateral corner of the skull table is formed subequally by the supratemporal and the tabular. As indicated by Berman (2000), character state 7(1) represents a modification of character state 2(1) of Berman et al. (1992), with the other two states (0, posterolateral corner of the skull table formed entirely by the tabular; and 2, posterolateral corner of the skull table formed almost entirely by the parietal and partly by a greatly reduced supratemporal) of characters 7 and 2 remaining identical. The posterolateral corner of the skull table in all diadectomorphs except *Tseajaia*, as discussed above, is indeed formed subequally by the supratemporal and tabular, but that of synapsids is formed entirely or nearly entirely by the supratemporal. Thus, whereas Diadectomorpha was incorrectly coded for character 2 of Berman et al. (1992), it is properly coded for character 7 of Berman (2000), and whereas Synapsida was correctly coded for character 2 of Berman et al. (1992), it is incorrectly coded for character 7 of Berman (2000). Character states 7(1) and 2(1) of Berman (2000) and Berman et al. (1992) can therefore not be regarded as a synapomorphy uniting Diadectomorpha and Synapsida.

The second character state [6(1)] of Berman (2000) to link diadectomorphs to synapsids was refuted by Laurin and Reisz (1995) after its first description by Berman et al. [1992; 5(1)], as indicated above, and the first character [5(2)] is also questionable. Examination of YPM 811 indicates that the tabular of *Limnoscelis* does not contact the paroccipital process of the opisthotic to enclose a small posttemporal fenestra (*contra* Berman 2000). The occipital regions of UCMP 59012, the holotype of *Tseajaia campi*, and FMNH UC 675, the only specimen of *Diasparactus* to possess the skull, are imperfectly preserved, leaving the relationship between the tabular and opisthotic uncertain in both taxa. Although Vaughn (1972; fig. 4) described the presence of a fenestra

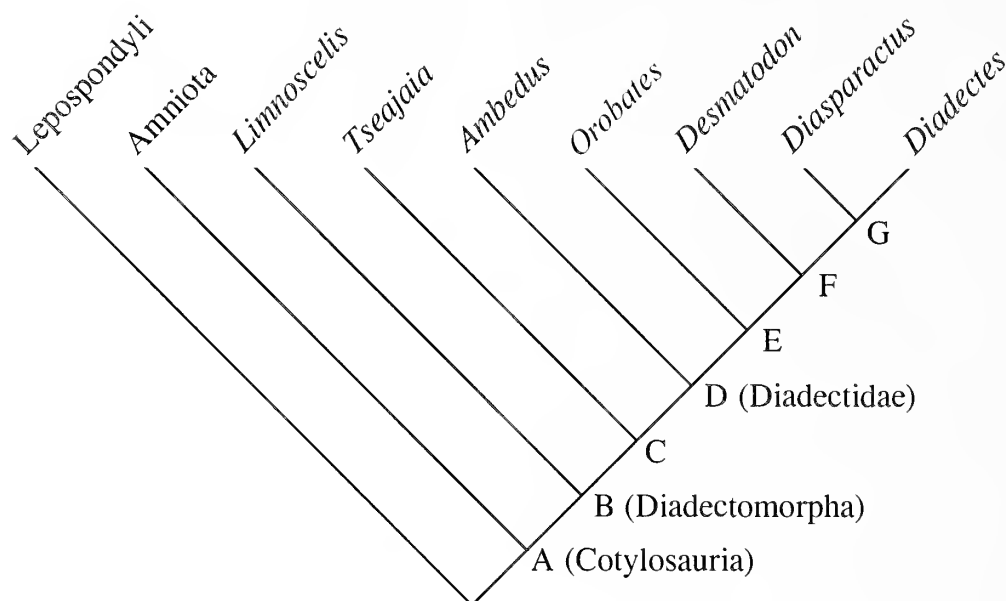


Fig. 6.—Hypothesis of diadectomorph interrelationships. Autapomorphies of the clades and terminal taxa are as follows, with all characters listed possessing an unambiguous history: Node A (Cotylosauria): 5(1), 33(1), 35(1); Amniota: 1(1), 11(1), 24(1); Node B (Diadectomorpha): 2(1), 4(1), 18(1), 25(1), 26(1), 32(1), 36(1), 37(1); Node C: 3(1), 8(1); Node D (Diadectidae): 27(1), 30(1), 31(1); Node E: 22(1), 26(2), 28(1); Node F: 12(1); 20(1); Node G: 19(1), 22(2), 30(2), 31(2).

tra between the postparietal and tabular in *Desmatodon hesperis*, no fenestra is located between the tabular and opisthotic. Thus, if Berman's (2000) interpretation of the occipital region of *Diadectes* is correct, then the presence of character [5(2)] in *Diadectes* and some synapsids is likely the result of convergence.

With most of the characters used by Berman et al. (1992) and Berman (2000) to link diadectomorphs and synapsids either refuted or in question, the recognition of diadectomorphs and synapsids as sister-taxa is not well supported. Rather, based on the more inclusive analyses performed by Gauthier et al. (1988), Laurin and Reisz (1995, 1997, 1999), and Lee and Spencer (1997), which employed much larger data matrices than those of Berman et al. (1998) and Berman (2000), Diadectomorpha is regarded as the sister-taxon to Amniota, not a member of it.

CONCLUSIONS

Phylogenetic analysis supports previous hypotheses that *Limnoscelis*, *Tseajaia*, and Diadectidae form a monophyletic group (Diadectomorpha), with diadectids and *Tseajaia* sharing a more recent common ancestor than either does with *Limnoscelis*. This analysis is the first to

consider the interrelationships of Diadectidae, which was found to represent a monophyletic group consisting of (*Ambedus* (*Orobates* (*Desmatodon* (*Diasparactus* + *Diadectes*))). Inclusion of more data will further test this hypothesis of relationships.

The description of *Ambedus pusillus* increases the total number of currently recognized diadectid taxa to seven genera and thirteen species: *Diadectes sideropellicus* Cope 1878; *Diadectes tenuitectes* (Cope 1896); *Diadectes lentus* (Marsh 1878); *Diadectes carinatus* (Case and Williston 1912); *Diadectes sammiguelensis* Lewis and Vaughn 1965; *Diadectes absitus* Berman et al. 1998a; *Diasparactus zenos* Case, 1910; *Desmatodon hollandi* Case, 1908; *Desmatodon hesperis* Vaughn, 1969; *Phanerosaurus naumanni* Meyer, 1860; *Stephanospondylus pugnax* (Geinitz and Deichmüller 1882); *Orobates pabsti* Berman et al., 2004; and *Ambedus pusillus*. As previously indicated, the affinity of the diadectid remains from Richards Spur are uncertain at this time. With the recognition of Limnoscelidae as a monogeneric taxon (Wideman 2002), the Permian-Carboniferous clade Diadectomorpha consists of (*Limnoscelis* (*Tseajaia* + Diadectidae)) (Fig. 6). Only two species of *Limnoscelis*, *L. paludis* Williston, 1911 and *L. dynatis* Berman and Sumida, 1990, are currently recog-

nized, and *Tseajaia* is a monospecific genus, with *T. campi* Vaughn, 1964 as its only member. Thus, if the number of species associated with sister-taxa Diadectidae and *Tseajaia* is considered, it is found that members of Diadectidae constitute the majority of species within that clade, an asymmetry of species-richness that suggests an evolutionary radiation of Diadectidae.

Based on cranial, dental, and postcranial anatomy, members of Diadectidae are thought to represent the earliest known examples of vertebrates capable of processing a diet of high-fiber terrestrial plants (Hotton et al. 1997; Sues and Reisz 1998; Reisz and Sues 2000). As the first terrestrial vertebrate herbivores, diadectids inhabited previously unoccupied ecological space. It is therefore hypothesized that the evolution of high-fiber herbivory in Diadectidae led to the radiation of species within that group, producing a clade that is markedly more species-rich than other diadectomorph taxa. *Ambedus pusillus* is unique among diadectids in its high maxillary and mandibular tooth counts, lack of incisiform anterior teeth, shallow dentary, lack of a labial parapet, relatively shallow alveolar shelf suggesting the presence of teeth with roots shorter than the height of the crown, and lesser degree of molarization of the cheek teeth. Despite lacking a deep lower jaw, which is characteristic of herbivores and found in other diadectids, the presence of procumbent anterior teeth, molariform cheek teeth, and wear facets similar to those of other diadectids suggest that *Ambedus*, like all other diadectids, may have been herbivorous. However, in the absence of additional material, such as postcranial and more complete skull remains, it is not possible to determine if *Ambedus* was a high-fiber herbivore, and it is therefore not possible to determine if the acquisition of high-fiber herbivory evolved within Diadectidae. In addition, with the validity of several diadectid species in question (e.g., *Phanerosaurus naumanni* and *Stephanospondylus pugnax*; Berman et al. 1998a), further evaluation of diadectid phylogeny and patterns of diadectid temporal and geographic distribution are required before the evolutionary history of Diadectidae is resolved.

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TABLE 1. Maximum crown measurements (in mm) and ratios of largest preserved, midseries maxillary cheek teeth in selected specimens of *Diadectes*, *Desmatodon*, *Orobates*, and *Ambedus*. Modified from Berman and Smitida (1995).

	Maximum transverse width	Maximum anteroposterior length	Maximum height	Length/Width	Height/Width
<i>Diadectes lentus</i> FMNH UC 675 (positions 6 to 8)	13.6	5.3	5.5	0.39	0.40
<i>Desmatodon hesperis</i> CM 47654 (holotype; positions 7 and 8); CM 47677 seventh posteriormost preserved tooth)	7.8; 9.3	5.3; 4.5	8.5; 8.0	0.68; 0.48	1.09; 0.86
<i>Desmatodon hollandi</i> CM 1938 (holotype; ?eighth posteriormost preserved tooth)	9.5	4.3	7.0	0.45	0.74
<i>Desmatodon aff. D. hollandi</i> YPM 8639 (CM 38044; positions 9 to 11)	9.5	4.3	7.0	0.45	0.74
<i>Orobates pabsti</i> MNG 11134 (positions 6 to 8)	5.4	1.8	6.0	0.33	1.11
<i>Ambedus pusillus</i> MCZ 9436 (holotype; tooth 9; tooth 8)	2.11; 1.94	1.06; 1.10	1.86; 1.91	0.50; 0.57	0.88; 0.99

TABLE 2. Maximum crown measurements (in mm) and ratios of largest preserved, midseries dentary cheek teeth in selected specimens of *Diadectes*, *Desmatodon*, *Orobates*, and *Ambedus*. Modified from Berman and Smitida (1995) and Kissel and Lehman (2002).

	Maximum transverse width	Maximum anteroposterior length	Maximum height	Length/Width	Height/Width
<i>Diadectes lentus</i> FMNH UC 675 (probable positions 8 to 10)	11.6	4.7	5.5	0.41	0.47
<i>Diasparactus zenos</i> OMNH 55350 (tooth 10)	13.0	5.0	5.5	0.38	0.42
<i>Desmatodon hesperis</i> CM 47670 (positions 9 to 11); CM 47661 (isolated crown)	8.8; 10.5	4.7; 5.7	7.0; 6.8	0.53; 0.54	0.80; 0.65
<i>Orobates pabsti</i> MNG 11134 (tooth 14)	5.3	2.7	6.4	0.51	1.21
<i>Ambedus pusillus</i> MCZ 9440 (sixth posteriormost tooth position; fifth posteriormost tooth position)	1.35; 1.35	1.10; 1.01	1.69; 1.69	0.82; 0.75	1.3; 1.3

APPENDIX 1. *List of characters used in this study. No characters were ordered. Characters incorporated from other studies are referenced, with the original number of the character from a particular study indicated.*

- 1) Frontal: excluded from orbit (0); contacts orbit between prefrontal and postfrontal (1). (Laurin and Reisz 1997, 8).
- 2) Lateral parietal lappet: absent (0); present (1).
- 3) Parietal foramen diameter: less than 33% (0) or 33% or greater than the anteroposterior length of the parietal midline suture (1).
- 4) Postparietal: paired (0); single and median (1). (modified from Laurin and Reisz 1995, 4; Laurin and Reisz 1997, 22).
- 5) Postparietal position: on skull table or on skull table and occiput (0); only on occiput (1). (Laurin and Reisz 1997, 23; Lee and Spencer 1997, 11).
- 6) Tabular: large, on skull table and occiput (0); reduced, on skull table and occiput (1); reduced, nearly to entirely occipital (2).
- 7) Posterolateral corner of skull table: formed entirely by tabular (0); formed entirely or nearly entirely by supratemporal (1); formed subequally by the supratemporal and tabular (2). (modified from Berman et al. 1992, 2; Berman 2000, 7).
- 8) Vertical, shallow temporal notch: absent (0); present (1).
- 9) Internal nares: short (0); long, where the ratio of the anteroposterior length of the internal nares to the length of the skull table 33% or greater (1).
- 10) Denticles on palate: present (0); absent (1). (Laurin and Reisz 1997, 53).
- 11) Three distinct rows of teeth on palate: absent (0); present (1).
- 12) Secondary palatal shelf formed by palatine and ectopterygoid: absent (0); present (1).
- 13) Palatal ramus of pterygoid makes substantial contribution to posterior medial border of internal naris and prevents a palatine-vomer contact: absent (0); present (1). (Berman et al. 1998a).
- 14) Medial row of teeth on palatal ramus of pterygoid: absent (0); present (1).
- 15) Transverse flange of pterygoid: lies at approximately the same level as the palate (0); projects ventrally to or below the level of the maxillary dentition (1).
- 16) Well-developed teeth on the margin of the transverse flange of the pterygoid: absent (0); present (1).
- 17) Contact between supratemporal and the dorsal margin of the paroccipital process of opisthotic: absent (0); present (1). (Berman et al. 1998a)
- 18) Otic trough in ventral flange of opisthotic: absent (0); present (1). (Laurin and Reisz 1995, 58).
- 19) Position of jaw articulation: at approximately the same level as the occlusal plane (0); ventral to the occlusal plane (1).
- 20) Deep lower jaw: absent (0); present, where the ratio of the dorsoventral height of the mandible at the level of the coronoid eminence to the anteroposterior length of the jaw is 33% or greater (1). With the exception of *Diadectes absitus*, all species of *Diadectes* possess a deep lower jaw. Because of this and other features detailed by Berman et al. (1998a), the diadectid specimens described as *D. absitus* are quite distinct from those of North American *Diadectes* species. These differences suggest the need to reexamine the specimens described as *D. absitus* and their assignment to the genus *Diadectes*, but until this issue is explored by the current authors with a detailed phylogenetic analysis of Diadectidae, *D. absitus* is recognized herein, and the genus of *Diadectes* is coded as possessing a deep lower jaw. If future analyses support the inclusion of this material into the genus *Diadectes*, then the shallow lower jaw in *D. absitus* is likely an autapomorphy of that form, as indicated by Berman et al. (1998a).
- 21) Meckelian fenestra: absent (0); elongate (1); tall, where the ratio of the greatest dorsoventral height to the anteroposterior length is 25% or greater (2).
- 22) Labial parapet: absent (0); low, where the parapet never projects higher than the bases of the cheek teeth (1); tall, where the parapet is as tall or taller than the occlusal surface of the teeth near the posterior end of the tooth row (2). This character, like 20, is problematic within the genus *Diadectes*. All examined specimens of *Diadectes* recovered from North America possess a tall labial parapet, but those from Germany described as *Diadectes absitus* possess a low labial parapet. As indicated in the discussion of character 20, the taxonomic status of *D. absitus* will be examined in order to further resolve this issue.
- 23) Anterior process of articular: absent (0); present (1).
- 24) Coronoid teeth: present (0); absent (1).
- 25) Infolding of dentine: absent (0); present (1). (Gauthier et al. 1988, 44; Laurin and Reisz 1995, 68).
- 26) Deep marginal tooth roots: absent (0); present, with root length less than crown height (1); present, with root length greater than crown height (2).
- 27) Heterodont dentition, characterized by the presence of transversely expanded cheek teeth: absent (0); present (1).
- 28) Anterior teeth: conical (0); incisiform (1).
- 29) Procumbent anterior teeth: absent (0); present in the lower jaw only (1); or present in both upper and lower jaws (2).
- 30) Degree of molarization of largest preserved, midseries dentary cheek teeth: absent (0); low (1); high, where the degree of molarization is considered high if the ratio of anteroposterior length to mediolateral width and dorsoventral height to mediolateral width are both less than 0.50 (2).
- 31) Labial and lingual cusps of cheek teeth: absent (0); weakly developed, represented by shoulders (1); or well developed (2).
- 32) Anterior process of axial intercentrum-atlantal pleurocentrum complex: absent (0); present (1). (Sumida et al. 1992, 9; Laurin and Reisz 1995, 84; Laurin and Reisz 1997, 111).
- 33) Neural arches of dorsal vertebrae: flat or concave (0); swollen (1). (Laurin and Reisz 1997, 107; Sumida and Modesto 2001).
- 34) Neural spines: short (0); tall, where the ratio of neural spine height to vertebral height is greater than 40% (1).
- 35) Sacrum composed of one (0), or at least two (1) vertebrae. (Gauthier et al. 1998, 65; Laurin and Reisz 1997, 119).
- 36) Lateral shelf on iliac blade: absent (0); present (1). (Heaton 1980; Laurin and Reisz 1995, 107).
- 37) Humerus with a distinct shaft (0), or short and robust, without a distinct shaft (1). (modified from Laurin and Reisz 1995, 104).

APPENDIX 2. *Data matrix used in this study.*

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3																																								
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7				
Lepospondyli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Amniota	1	0	0	0	1	2	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0			
<i>Limnoscelis</i>	0	1	0	1	1	1	2	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1			
<i>Tseajaia</i>	0	1	1	1	1	1	1	1	0	0	0	0	1	0	0	?	1	0	0	2	0	0	0	1	1	0	0	0	0	0	1	1	0	1	1	1	1				
<i>Ambodus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	1	0	?	1	1	?	?	?	?	?	?				
<i>Orobates</i>	0	1	1	1	1	2	1	?	0	0	0	?	1	0	0	1	1	0	0	2	1	0	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1				
<i>Desmatodon</i>	?	1	1	1	1	2	1	?	0	0	1	?	1	1	0	1	1	0	1	2	1	1	1	1	2	1	1	1	1	1	?	1	1	?	?	?	1				
<i>Diasparactus</i>	?	?	?	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1	1	?	2	?	?	?	1	2	1	?	?	?	2	2	1	1	1	1	1
<i>Diadectes</i>	0	1	1	1	1	2	1	0	1	0	1	1	1	1	0	1	1	1	1	2	2	1	1	1	2	1	1	2	2	2	1	1	0	1	1	1	1	1			

REVISION OF THE FLEA GENUS *JELLISONIA* TRAUB, 1944 (SIPHONAPTERA: CERATOPHYLLIDAE)

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ABSTRACT

The flea genus *Jellisonia* Traub, 1944, is revised with recognition of two subgenera (*Jellisonia* Traub and *Pleochaetoides* Augustson), description of two new species and one new subspecies (*Jellisonia eckerlini*, *Jellisonia maxwelli*, and *Jellisonia breviloba barrerae*), new synonymy of two species (*Jellisonia dybasi* Traub, 1950 = *Jellisonia klotsi* Traub, 1944; *Jellisonia bonia* Traub and Johnson, 1952 = *Jellisonia wisemani* Eads, 1951), three new combinations (*Kohlsia falcata* Méndez and Hanssen, 1975 = *Jellisonia falcata*; *Kohlsia tiptoni* Méndez and Altman, 1960 = *Jellisonia tiptoni*; *Jellisonia ortizi* Vargas, 1951 = *Kohlsia ortizi*), and change of status for one species (*Jellisonia hayesi breviloba* Traub, 1950 = *Jellisonia breviloba*). The northern and southern extremes for the genus *Jellisonia* are Dallas County, Texas, U.S.A., and Meta Department, Colombia, respectively. A generic key to *Jellisonia* and allied genera (*Baculomeris* Smit, 1983; *Kohlsia* Traub, 1950; *Pleochaetis* Jordan, 1933; *Phsaetis* Smit, 1983) and including subgenera and known species of *Jellisonia*, is provided. Distribution maps are given for all species of *Jellisonia*. Fifty-eight percent of the specimens examined (736/1261), were collected between 1960 and 1969, while only 16% (203/1261) were collected after 1969. The current number of valid species-group taxa in *Jellisonia* is 17.

KEY WORDS: *Jellisonia*, *Kohlsia ortizi*, new species, geographic distribution, fleas, taxonomy

INTRODUCTION

The flea genus *Jellisonia* has received little attention from revisionary systematists, although specialists have continued to describe new species intermittently following the original description of the genus. In December 1944, both Traub and Augustson published descriptions of new genera based on species now considered to be congeneric in *Jellisonia*, specifically *Jellisonia klotsi* Traub (1944) and *Pleochaetoides bullisi* Augustson (1944). Traub's publication was dated 20 December 1944 and Augustson's issue was dated December 1944. Traub (1950) correctly synonymized *Pleochaetoides* with *Jellisonia*. Lewis (1990) listed 12 valid species-group taxa in *Jellisonia* (*J. amadoi* Ponce-Ulloa, 1988; *J. bonia* Traub and Johnson, 1952; *J. bullisi* (Augustson 1944); *J. dybasi* Traub, 1950; *J. grayi* Hubbard, 1958; *J. hayesi hayesi* Traub, 1950; *J. h. breviloba* Traub, 1950; *J. ironsi* (Eads 1947); *J. johnsonae* Tipton and Méndez, 1961; *J. klotsi* Traub, 1944; *J. mexicana* Ponce-Ulloa, 1988; *J. wisemani* Eads, 1951) but overlooked *Jellisonia ortizi* Vargas, 1951. Morales (1990) subsequently described *Jellisonia guerrerensis* and Hastriter and Eckerlin (2003) described *Jellisonia painteri*. Prior to the current revision, there were 15 recognized species-group taxa (including subspecies) in the genus.

The author recently obtained a small collection of fleas from Oaxaca, Mexico, which included specimens of *Jellisonia*. Attempts to identify these specimens proved difficult and enigmatic without up-to-date keys and no modern treatment of the genus. Traub's (1950) key to the species known at that time included only six names. Additional keys to include the eight subsequently described species did not exist. The systematic status of several species within *Jellisonia* and the closely allied

genus *Kohlsia* were questionable. Factors making the revision of *Jellisonia* difficult include: 1) very few records existed for the Central American countries of Belize, Costa Rica, Honduras, and Nicaragua; 2) systematics of the mammalian hosts were poorly understood during the period of greatest collecting activity (1950s and 1960s) and the host data on many specimens indicate only a generic identification (recent research using DNA sequence data and karyotyping will undoubtedly make some of these erroneous); 3) many flea specimens had been poorly mounted, making their study difficult; and 4) there was no alcohol-preserved material for preparing dissections desirable for detailed studies.

Jellisonia belongs to the family Ceratophyllidae and representatives are distributed from north central Texas, U.S.A., to northern Panama (one species recorded in Colombia). These fleas are usually montane species parasitizing small murid rodents belonging to the subfamily Sigmodontinae, e.g., species of *Baiomys* True, *Habromys* (Hooper and Musser), *Megadontomys* Merriam, *Neotoma* Say and Ord, *Neotomodon* Merriam, *Nyctomys* Saussure, *Oryzomys* Baird, *Osgoodomys* Hooper and Musser, *Peromyscus* Gloger, *Reithrodontomys* Giglioli, *Scotinomys* Thomas, *Sigmodon* Say and Ord, and *Tylomys* Peters. With few exceptions, species of *Jellisonia* are not always host specific on this group of mammals, and are occasionally found on small mammals other than sigmodontines (specimens were examined in this revision from *Bassariscus* Coues, *Chaetodipus* Merriam, *Cryptotis* Pomel, *Didelphis* Linnaeus, *Dipodomys* Gray, *Liomys* Merriam, *Microtus* Schrank, *Mus* Linnaeus, *Nyctinomys* Miller, *Rattus* Fischer, *Sorex* Linnaeus, and *Tamandua* Gray). Flea genera most closely allied to *Jellisonia*

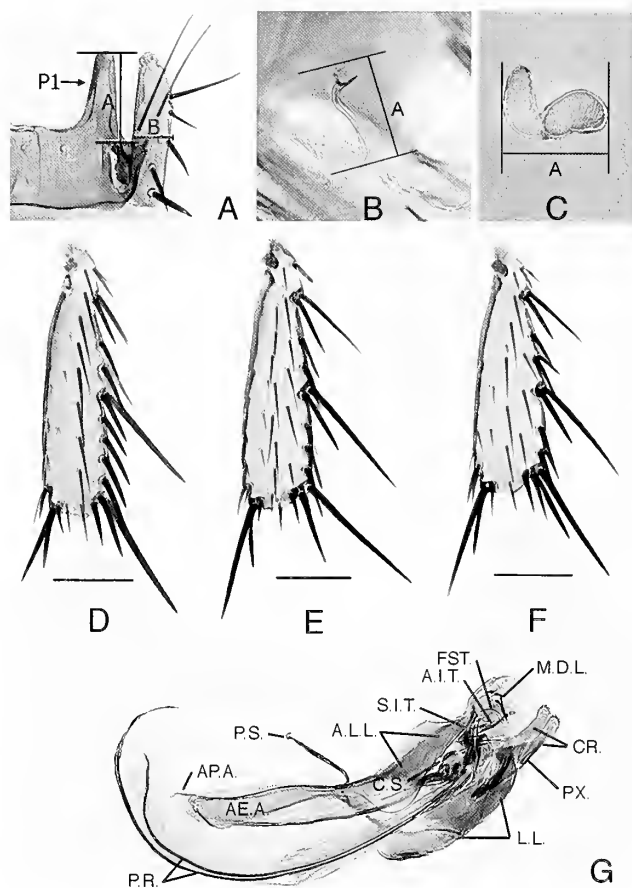


Fig. 1.—Morphological features of *Jellisonia*: A, Male tergum IX [A = length of process I (P1), B = width of telomere]; B, Bursa copulatrix (A = length); C, Spermatheca (A = length); D, Metatibia of *J. klotzi*; E, Metatibia of *J. bullisi*; F, Metatibia of *J. ironsi*; G, Aedeagus of *J. klotzi* (A.L.L., accessory lateral lobe; A.E.A., aedeagal apodeme; APA., apical appendage; A.I.T., armature of sclerotized inner tube; C.S., crescent sclerite; CR., crochet; F.S., Ford's sclerite; FST., fistula; L.L., lateral lobe; M.D.L., median dorsal lobe; PX., paxillus; P.R., penis rods; P.S., proximal spur of aedeagus).

include *Baculomeris* Smit (1983), *Kohlsia* Traub (1950), *Pleochaetis* Jordan (1933), and *Plusaetis* Smit (1983). *Jellisonia* is sympatric with each of these genera throughout much of their ranges. During this revision, the author studied specimens from many localities not previously published in the literature. Geographical records documented in this revision under "Material Examined" contribute greatly to an understanding of species distributions and provide a basis for identifying geographical gaps in the range of *Jellisonia* species that should be a focus for future field research.

MATERIALS AND METHODS

An understanding of the complicated aedeagus and associated anatomy of the modified abdominal segments of the male requires dissection. Alcohol specimens were not available for any of the species studied; therefore, dissec-

tions were prepared from existing slide-mounted material. Slide mounted specimens were selected and placed in petri dishes in xylene until the Canada balsam medium was dissolved sufficiently to free the specimens (usually overnight). Dissections were made in xylene by removing the right tergum IX, aedeagus, and sternites VIII and IX with *minuten nadeln* mounted on the tips of applicator sticks. Because of their extremely small size, these anatomical parts were picked up under one dissecting scope with a micro-spatula and transferred onto a microscope slide in a small drop of Canada balsam under another dissecting microscope. The remaining whole flea was mounted on the same slide as the dissected parts under a second cover slip.

Two ratios were used in the study to discriminate some species. The first was the ratio of the length of the process I of the telomere (P1) to the width of the telomere ($\text{Length of P1/Width of Telomere} = \text{Ratio}$) (Fig. 1A). The length of P1 was measured from the upper portion of the condyle of the telomere to the apex of P1. The width of the telomere was measured at the level of the third marginal spiniform seta (counting from proximal to distal). The second ratio was the length of the sclerotized portion of the bursa copulatrix compared to the length of the spermatheca (Fig. 1B–C). The overall body dimensions were measured from the foremost portion of the frons to the posterior margin of the telomere in males, and to the posterior border of the sensillar plate in females. Anatomical terminology follows that of Rothschild and Traub (1971) and new terminology described in Hastriter and Eckerlin (2003).

Specimens of *Jellisonia* were gathered from many institutions. Following is a listing of those institutions with their associated acronyms. Throughout the text, these acronyms are placed in parentheses after the "Type Species" or "Material Examined" sections to designate repository or collection where specimens are maintained. All specimens with data preceding the acronym belong to that institution: AMNH—Division of Invertebrate Zoology, American Museum of Natural History, New York, New York; BMNH—Department of Entomology, The Natural History Museum, London, England; BYU—Brigham Young University Flea Collection, Monte L. Bean Life Science Museum, Provo, Utah; CMNH—Section of Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CNC—Canadian National Collections of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada; FMNH—Division of Insects, Field Museum of Natural History, Chicago, Illinois; FSCA—Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida; GML—Gorgas Memorial Laboratory (formerly), Balboa, Panama; INDRE—Instituto de Diagnóstico y Referencia Epidemiológicos (formerly Instituto de Salubridad y Enfermedades Tropicales), Mexico City, Mexico;

MWH—Personal Collection of Michael W. Hastriter, Monte L. Bean Life Science Museum, Provo, Utah; REL—Personal Collection of Robert E. Lewis, Professor Emeritus, Iowa State University, Ames, Iowa; RPE—Personal Collection of Ralph P. Eckerlin, Professor, Northern Virginia Community College, Annandale, Virginia; UNAM—Museo de Zoología, Universidad Nacional Autónoma de México, Mexico City, Mexico; USNM—Division of Systematic Biology-Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Distribution maps were constructed using ArcView GIS 3.3 for Windows and Adobe Photoshop 7.0. Line drawing illustrations were prepared with the aid of a Ken-A-Vision™ Microprojector, Model X1000-1. An Olympus BX61 Compound Microscope, Olympus CV12 digital camera, Olympus Microsuite™ B3SV program, and Adobe Photoshop 7.0 were used to prepare digitized images.

SYSTEMATIC ACCOUNT

Order Siphonaptera
Family Ceratophyllidae

Genus *Jellisonia* Traub, 1944

Jellisonia Traub, 1944.

Type Species: *Jellisonia klotzi* Traub, 1944. Field Museum of Natural History, Zoological Series, 29: 211–214 (FMNH) (by monotypy).

Pleochaetoides Augustson, 1944.

Type Species: *Pleochaetoides bullisi* Augustson, 1944. Journal of Parasitology, 30: 366–368 (by monotypy).

Structural characters used to distinguish the vast majority of species belonging to the Ceratophyllidae are found in males. Females are very similar in appearance and often cannot be reliably distinguished without accompanying males or by their geographic distribution. *Jellisonia* is no exception. The most stable and representative characters for most species of *Jellisonia* are found in the modified segments of the male (tergum IX, sternum IX, and the aedeagus). The caudal margin of sternum VII of females may be highly variable within the same population of some species but is consistent and useful in other species. The spermatheca offers little basis for taxonomic discrimination across the genus. The bulga and hilla are usually subequal in length. The hilla of any one species may or may not possess an apical papilla. The shape and length of the bursa copulatrix is useful in discriminating between some species.

Diagnosis.—This species is closely related to *Kohlsia*, from which it is distinguished in the male by the presence of an apical appendage on the aedeagal apodeme, two inverse setae on the distal arm of sternum IX, and tubercles at the apex of the crochet. The bulga is longer than wide with sides somewhat parallel (convex dorsally and

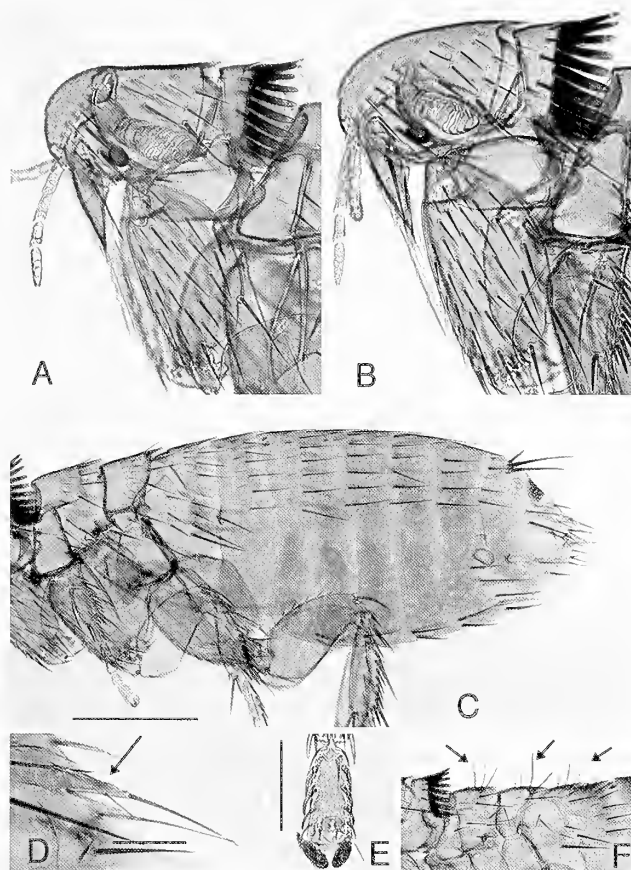


Fig. 2.—A–E, *Jellisonia painteri*: A, Head, male; B, Head, female; C, Thorax and abdomen, female; D, Anal stylet, arrow; E, Fifth segment of hind tarsi; F, *Jellisonia amadori*, thorax (arrows indicate “mane”). (Scale = A–D, F are 200μ; E is 100μ).

usually concave ventrally), while the spermatheca of *Kohlsia* is more globular. Other genera often confused with *Jellisonia* are *Baculomeris*, *Plusaetis*, and *Pleochaetis*. Males of *Jellisonia* are readily separable from these genera by the presence of one guard seta at the apex of the fore femur, the absence of an incision or cleavage on the ventral margin of the distal arm of sternum IX (forming two lobes), and lack of Wagner’s organ. Females are distinguished by the chaetotaxy of the anal stylet, which bears only a minute dorsal seta, a long apical seta, and a long ventral seta (a character shared by *Kohlsia*) (Fig. 2D).

Description.—**Head** (Fig. 2A–B). Frons evenly rounded, frontal tubercle present but small. Longitudinal dorsal sulcus of occipital area present but shallow in male. Antennal sulcus absent in female, present in male. Preantennal and postantennal areas each with three rows of setae, variable numbers in each row; preantennal area occasionally with fourth row of a single seta. Surface area punctate anterior to first row; smooth posterior to row. Oral angle with small incassation; one or two setae below angle. Maxilla acutely pointed, maxillary palpus with five segments, never exceeding apex of fore coxa. Antennal pedicel not ensheathing clavus, with fringe of short setae; terminal one or two segments of clavus extending onto prosternum in male. Eye well developed, darkly pigmented, not sinuate. Genal process subacute; genal teeth lacking. Setae in fringe along dorsal margin of antennal fossa few,

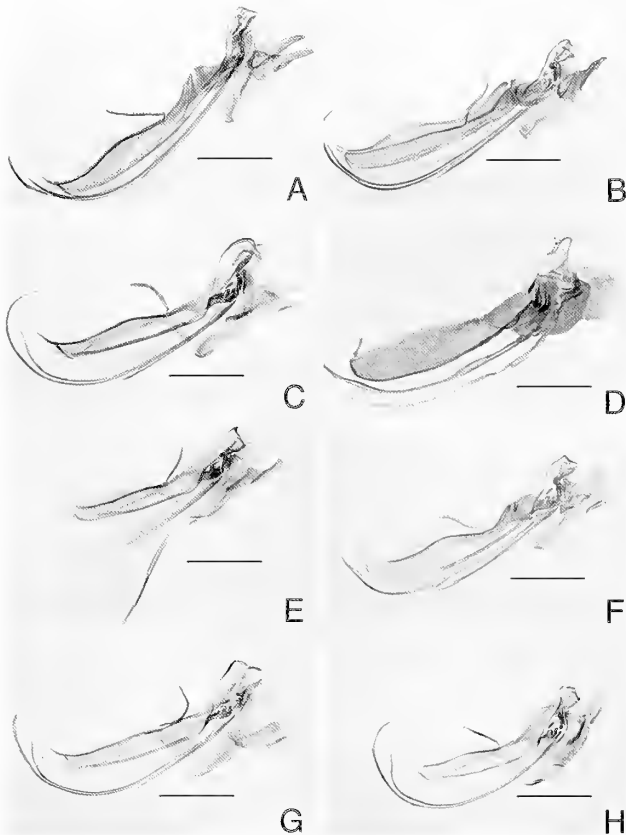


Fig. 3.—Aedeagi of *Jellisonia* species: A, *J. breviloba barrerae*, n. ssp.; B, *J. b. breviloba*; C, *J. eckerlini*, n. sp.; D, *J. falcata*; E, *J. guerrenensis*; F, *J. hayesi*; G, *J. johnsonae*; H, *J. klotsi*. (Scale = 200 μ).

variably distributed. **Thorax** (Fig. 2C, F). Pronotum narrow, width much less than length of 18–20 spines; with single row of setae. Prosternum with notch for cervical link plate. Mesonotum with three rows of setae and scattered anterior setae; mesonotal collar with variable numbers of pseudosetae. Mesopleural rod bifurcate dorsally. Lateral metanotal area with two setae. Metanotum with three rows of setae, with or without apical spinelets; notal ridge well defined. Metapleural rod thick, pleural arch well developed. Metepisternum and metasternum with an incomplete sclerotized division. Metepisternum with squamulum. Metepimeron with three vertical rows of setae, posterior two rows ventral to spiracle. **Legs** (Fig. 1D–F, 2E). Fore femur with numerous lateral setae and one mesal seta. Dorsal margin of fore tibia with false comb. Dorsal margins of mesotibia and metatibia with or without false combs; if with false combs, single lateral row of setae (otherwise double). Caudal margin of fore tarsal segment I with “comb” of three setae. Five pairs of lateral plantar bristles, proximal pair shifted onto plantar surface. Two preapical plantar bristles, hair-like or subspiniiform. Oblique break line of mesocoxa incomplete. Metacoxa without patch or row of spiniiform setae or any setae on mesal surface; anterior margin adorned with fine setae. Ventrocaudal margin of metacoxa with incised notch. **Unmodified Segments of Abdomen** (Fig. 2C). Marginal spinelets on tergites I–III, sometimes IV; tergites II–VII with two rows of setae, one seta below level of spiracle on each. Spiracular fossa round. Antsensillial bristles three, although mesal and lateral bristles of males may be minute. Sternum II with one seta on each side; sternites III–VI with either two or three on each side. **Modified Segments of Male** (Fig. 1G, 3–17). Tergum VIII enveloping whole of tergum IX; setal arrangements variable. Basimere of tergum IX variably extended caudad with triangular or finger-like process PI above articulation of telomere. Two aetabular bristles emerging near acetabulum, arising from lobe or not. Telomere bear-

ing three to six marginal setae, either slender or spiniiform. Sternum VIII vestigial, pencil-like or more developed, with or without setae. Apex of sternum VIII with or without membranous extensions. Spiculated intersegmental membrane connecting sternites VIII and IX apparent in some species, absent in others. Proximal portion of distal arm of sternum IX, (about one-third to one-half length) sclerotized, not lobate; distal portion variously expanded with a mesal sclerotized longitudinal groove. Membranous area at juncture of proximal and distal portions of distal arm of sternum IX (appears to be a point of flexure for distal portion of distal arm). Paired distal arms of sternum IX fused to flexure point some distance beyond. Lateral apical aspect of sternum IX with two setae directed cephalad [termed ventral and dorsal inverse setae by Hastriter and Eckerlin (2003)], dorsal inverse seta always small (absent in *Jellisonia falcata* and *Jellisonia tiptoni* although an alveolar pit is present). Apodemal rod of sternum IX present. **Aedeagus** (Fig. 1G, 3–8). Apodeme of aedeagus expanded in middle forming a mild dorsal convexity (lateral view); apex with apical appendage and proximal spur at anterior junction of aedeagal pouch (proximal spur connects phallosome to arched roof of tergum IX). External components of end chamber comprised of median dorsal lobe (multiple configurations), paired accessory lateral lobes, sclerotized portion (lateral view) appears acutely pointed (very short in *J. hayesi*, *J. b. breviloba*, vestigial in *J. b. barrerae*), paired lateral lobes usually sclerotized ventrally. Crochet hyper-developed; positioned along ventral floor of aedeagal pouch. Apex of crochet studied with spicules or tuberculate structures (termed micromucronate by Traub 1950); paxillus present. Crescent sclerite short, thickened in middle with satellite sclerite caudad. Sclerotized inner tube short, moderately sclerotized with paired armature of sheath of inner tube extending over sclerotized inner tube. Fistula present at apex of sclerotized inner tube; approximately equal length of latter. Penis rods extend beyond aedeagal apodeme but do not form a complete coil. **Modified Segments of Female** (Fig. 18–22). Tergum VIII large, chaetotaxy varies. Anal stylet of dorsal anal lobe 3–5 times as long as wide; single apical long seta; small ventral seta; and minute dorsal seta at apex sometimes present. Ventral anal lobe angulate with slender spiniiform setae. Sternum VII with complex of lobes and sinuses, no marked sclerotization on caudal margin. Sternum VIII inconspicuous, without setae (although minute hairs may adorn apex of some species). Bulga of spermatheca subequal in length to hilla, convex dorsally, concave ventrally; not globular. Bursa copulatrix sclerotized, straight, sigmoid, or undulate; upper one-fourth never flexed forward at right angle.

Remarks.—I have divided the genus into two subgenera based on chaetotaxy of the metatibia. The subgenera each tend to follow a different pattern of distribution. Although there is much overlap between them, members of the subgenus *Pleochaetoides* are most common in the northern range of the genus, whereas those of the subgenus *Jellisonia* are more abundant from central Mexico to the southern limits of the range of the genus. The most notable exception is that of *J. (P.) ironsi*, which spans much of the range of both subgenera, occurring from northern Texas to central Costa Rica. This may be attributed to its close association with its principle host, *Baiomys taylori* (Thomas 1887), whose range *J. ironsi* closely follows. Other species of *Jellisonia* are rarely found on *B. taylori*.

KEY TO THE SUBGENERA AND SPECIES OF *JELLISONIA* AND ALLIED GENERA

- I. Guard seta at apex of fore femur single. Male: Distal arm of sternum IX not divided into two lobes by an incision (cleft) on ventral margin and Wagner's organ is absent. Female: Anal stylet with minute dorsal seta (near apical seta), long apical seta, and long ventral sea 2

- 1'. Two guard setae present (mesal seta may be hidden behind the larger lateral seta). Male: Distal arm of sternum IX divided into two lobes and Wagner's organ present. Female: Anal stylet with long dorsal seta (set well cephalad of apex), apical and ventral setae same as above 3
- 2(1). Male: Two inverse setae present on dorsal margin towards apex of distal arm of sternum IX (Fig. 14C); apical appendage of aedeagal apodeme present (although short). Female: Bursa copulatrix usually subequal to length of spermatheca, straight or undulate (Fig. 22H-I), but perula never reflected cephalad at a right angle at distal one-fourth; bulga of spermatheca slightly concave beneath and convex dorsally, longer than wide (*Jellisonia*) 5 (Page 218)
- 2'. Male: Inverse setae and apical appendage absent. Female: Bursa copulatrix longer than length of spermatheca and perula reflected cephalad (Fig. 21B); bulga shorter, hilla relatively longer and more globular *Kohlsia*
- 3(1'). Most ventral seta in frontal row at same level of frontal tubercle (or nearly so) *Baculomeris*
- 3'. Ventral seta much lower than frontal tubercle, nearer base of maxillary palpus 4
- 4(3'). Male: Length of penis rods far exceeding apex of aedeagal apodeme, forming a full coil or more; apical appendage long (longer than maximum width of aedeagal apodeme); and apical half of telomere lacking short dark spiniform setae. Female: Proximal duct of spermatheca visibly dilated *Plusaetis*
- 4'. Male: Penis rods exceed length of aedeagal apodeme but are not substantially curved upward and do not form even a partial coil; apical appendage short (shorter than maximum width of aedeagal apodeme); one or more short, dark spiniform seta(e) present on ventroapical margin of telomere. Female: Proximal duct of spermatheca not noticeably dilated *Pleochaetis*
- 5(2). Metatibia with a false comb along dorsal margin. Metatibia with ten or more dorsal notches; a single seta in penultimate dorsal notch, and one vertical row of setae on lateral tibial surface (Fig. 1D) *Jellisonia* (*Jellisonia*) 6
- 5'. Metatibia without false comb along dorsal margin. Metatibia with eight or nine dorsal notches; two setae in penultimate dorsal notch, and two vertical rows of setae on lateral tibial surface (Fig. 1E-F) *Jellisonia* (*Pleochaetoides*) 25
- 6(5). Male 7
- 6'. Female 17

Males

- 7(6). Width of process one (P1) much greater than height. Telomere much wider apically than basally (Fig. 1A). Median dorsal lobe sclerotized and hook-like with ventral secondary lobe (Fig. 5D, 7A). Caudal margin of sternum IX adorned with 11–12 spiniform setae (Fig. 7A, 14D) (Guatemala to Colombia) 8
- 7'. P1 narrower and finger-shaped. Telomere usually narrows towards apex. Median dorsal lobe not hook-like and without a ventral secondary lobe. At most, 1–2 small spiniform setae on caudal margin of sternum IX (Fig. 14A, C) 9
- 8(7). Telomere with three large setae along caudal margin (Fig. 9D)(Colombia) *J. (J.) falcata* (Page 224)
- 8'. Telomere with four large setae along caudal margin (Fig. 10E)(Guatemala to northern Panama) *J. (J.) tiptoni* (Page 230)
- 9(7'). Median dorsal lobe not smoothly rounded and with a loop-like sclerotization intruding inward at anterodorsal margin (Fig. 5A–B, F). Crochet with round flask-shaped base (Fig. 5A–B). Small but distinct lobe on distal arm of sternum IX anterior to, or below level of ventral inverse seta (Fig. 13A–B), or lacking (Mexico) 10
- 9'. Median dorsal lobe smoothly rounded, without a loop-like sclerotization (Fig. 5C, 6A). Crochet linear, without round

flask-shaped base (Fig. 5C, E). Lobe on anterior margin of sternum IX never present (Fig. 13C, F)(Costa Rica, Guatemala, Mexico, or Panama) 13

- 10(9). Lobe on distal arm of sternum IX anterior to and on the same level as the ventral inverse seta (Fig. 14B) 11
- 10'. Lobe if present, below level of ventral inverse seta (Fig. 13A, B) 12
- 11(10). Apex of sternum IX forming an oblique 45° angle from ventral inverse seta to blunt apex (Fig. 14B). Sternum VIII pencil-like with setae (Fig. 17B) *J. (J.) maxwelli* n. sp. (Page 228)
- 11'. Apex of sternum IX convex along anterior margin above inverse seta and rounded at apex (Fig. 13E). Sternum VIII pencil-like without setae (Fig. 16E) *J. (J.) hayesi* (Page 225)
- 12(10'). Ventrocaudal margin of Ford's sclerite with distinct lobe (Fig. 5A). Sternum VIII with setae (Fig. 16A) *J. (J.) breviloba barrerae* n. ssp. (Page 221)
- 12'. Ford's sclerite strap-like without distinct lobe on ventrocaudal margin (Fig. 5B). Sternum VIII lacking setae (Fig. 16B) *J. (J.) breviloba breviloba* (Page 218)
- 13(9'). Apex of sternum IX abruptly turned caudad (like a hockey stick)(Fig. 13C, F) 14
- 13'. Apex of sternum IX not projecting caudad (Fig. 14C) 15
- 14(13). Apical sclerite of median dorsal lobe acutely pointed apically (Fig. 6A)(Costa Rica and Panama) *J. (J.) johnsonae* (Page 226)
- 14'. Apical sclerite round, narrowly blunt (Fig. 5C)(Costa Rica) *J. (J.) eckerlini* n. sp. (Page 222)
- 15(13'). Caudal margin of sternum IX with gentle convexity (Fig. 14C)(Guatemala) *J. (J.) painteri* (Page 229)
- 15'. Caudal margin of sternum IX with concavity in middle creating a proximal and distal lobe each bearing small spiniform setae (Fig. 13D–E, 14A)(Mexico) 16
- 16(15'). Marginal spiniform setae on telomere somewhat evenly spaced; distance between second and third spiniform setae (from proximal to distal) about equal or less than width of telomere at level of third spiniform seta. Caudal margin of telomere usually convex, or nearly straight. Ventral caudal lobe of telomere not particularly enlarged (Fig. 10B)(Mexico) *J. (J.) klotsi* (Page 227)
- 16'. Two most ventral marginal spiniform setae distinctly grouped and separated from more dorsal spiniform setae; distance between second and third spiniform setae distinctly greater than width of telomere at level of third spiniform. Caudal margin of telomere straight to slightly concave. Ventral caudal lobe of telomere more pronounced (Fig. 9E)(Mexico) *J. (J.) guerrereusis* (Page 224)

Females

- 17(6'). Caudal margin of sternum VII with a small, bluntly rounded lobe subtended by an obliquely concave margin extending to an acute ventral lobe (Fig. 20A)(Guatemala to northern Panama) *J. (J.) tiptoni* (Page 230)
- 17'. Ventral lobe usually rounded, sometimes truncate; never acute 18
- 18(17'). Sclerotized portion of bursa copulatrix sigmoid-shaped, much longer than length of spermatheca (1.5–2.0x longer)(Fig. 21D)(Colombia) *J. (J.) falcata* (Page 224)
- 18'. Bursa copulatrix not sigmoid-shaped, subequal to length of spermatheca (may be slightly shorter, or longer than spermatheca) 19
- 19(18'). Sternites IV–VI with two setae on each side (Fig. 18A) ... 20
- 19'. Sternites IV–VI with three setae on each side (Fig. 19A) ... 23
- 20(19). Dorsal lobe on caudal margin of sternum VII large (Fig. 18A, 19D) 21
- 20'. Dorsal lobe small or lacking entirely (Fig. 19B) 21

- *J. (J.) johnsonae* (Page 226)
- 21(20). Sinus on caudal margin of sternum VII as deep as, or deeper than width of lobe (from apex of sinus to closest margin of dorsal lobe) (Fig. 19D) 22
- 21'. Sinus on caudal margin shallow, less than width of lobe (Fig. 18A)(Costa Rica) *J. (J.) eckertini* n. sp. (Page 222)
- 22(21). Margin above dorsal lobe of sternum VII usually concave (Fig. 18C–H)(Mexico) *J. (J.) klotsi* (Page 227)
- 22'. Margin convex or lobe thickened (females indistinguishable except by geographic locality)(Fig. 18J)
 ...Guatemala: *J. (J.) painteri*, or Mexico: *J. (J.) gnerrensis* (Pages 229 and 224)
- 23(19'). Dorsal lobe on caudal margin of sternum VII large with subtending sinus (Fig. 19A, D) 24
- 23'. Dorsal lobe at most indicated; subtending sinus, if present, represented by shallow concavity (females of these three taxa are indistinguishable)(Fig. 19C)
 *J. (J.) b. breviloba*, *J. (J.) b. barrerae* n. ssp., and *J. (J.) maxwelli* n. sp. (Pages 218, 221, and 228)
- 24(23). Sclerotized portion of bursa copulatrix with perula reflected caudad (Fig. 22E) (Guatemala) *J. (J.) painteri* (Page 229)
- 24'. Bursa copulatrix straight, perula not reflected caudad (Fig. 22B)(Mexico) *J. (J.) hayesi* (Page 225)
- 25(5'). Males 26
- 25'. Females (unknown for *J. (P.) amadoi*) 31
- Males
- 26(25). Two apical setae on metatarsal segment I extending to, or beyond apex of metatarsal segment III. *(P.) amadoi* (Page 230)
- 26'. Apical setae much shorter, extending at most to apex of metatarsal segment II 27
- 27(26'). Metatibia with 8 dorsal notches (Fig. 1F) 28
- 27'. Metatibia with 9 dorsal notches (Fig. 1E) 30
- 28(27). Median dorsal lobe simple, not bifurcate (Fig. 7C). Sternum VIII vestigial and without seta (Fig. 16F) 29
- 28'. Median dorsal lobe bifurcate (Fig. 7B, D). Sternum VIII well developed and bearing at least one seta (Fig. 17F)
 *J. (P.) ironsi* (Page 232)
- 29(28). Ratio of length of P1 to width of telomere at level of third spiniform seta (counting from proximal) 1.3:1 (Fig. 1A). Median dorsal lobe narrowing towards rounded apex (Fig. 8A)
 *J. (P.) mexicana* (Page 233)
- 29'. Ratio of P1 and telomere 1:1. Median dorsal lobe more broadly rounded (Fig. 8B) *J. (P.) wisemani* (Page 235)
- 30(27'). Ratio of length of P1 to width of telomere 0.5:1 (Fig. 1A). Apex of P1 rounded. Entire condyle of telomere above level of acetabular bristles (Fig. 11A). Width of ventral inverse seta less than width of narrowest portion of distal arm of sternum IX; not lanceolate (Fig. 14E) *J. (P.) bullisi* (Page 231)
- 30'. Ratio of P1 and telomere 1.8:1. Apex of P1 acutely pointed. Most of the condyle below level of acetabular bristles (Fig. 11B). Width of ventral inverse seta equal to or greater than narrowest portion of distal arm of sternum IX; lanceolate (narrow at base, broad in middle, and abruptly acuminate at apex) (Fig. 14F) *J. (P.) grayi* (Page 232)
- Females
- 31(25'). Dorsal notch number seven (counting from proximal to distal) of metatibia with a single seta (Fig. 1F) 32
- 31'. Dorsal notch number seven of metatibia with two setae ... 33
- 32(31). Caudal margin of sternum VII with dorsal and ventral lobes forming a shallow sinus (Fig. 20C) ... *J. (P.) grayi* (Page 232)
- 32'. Caudal margin of sternum VII with only ventral lobe (Fig. 20B) *J. (P.) bullisi* (Page 231)

- 33(31'). Dorsal lobe of sternum VII short but acutely pointed. Sternites III–VI with two setae on each side (Fig. 20D)
 *J. (P.) ironsi* (Page 232)
- 33'. Dorsal lobe of sternum VII bluntly rounded. Sternites III–VI with three setae on each side (females are indistinguishable)(Fig. 21A)
 ... *J. (P.) wisemani* and *J. (P.) mexicana* (Pages 235 and 233)

Subgenus *Jellisonia* Traub 1944

Type Species: Jellisonia klotsi Traub, 1944. Zoological Series of Field Museum of Natural History, 29:211–214 (by monotypy and original designation).

Diagnosis.—Traub (1950) cited the presence of supernumerary spines (false combs) on the mesotibia and metatibia as one of the characteristics to define the genus, but a number of species described later do not have false combs. They are present on the dorsal margin of the mesotibia and metatibia of species in the subgenus *Jellisonia* (Fig. 1D) and absent in those placed in the subgenus *Pleochaetoides* (Fig. 1E–F). These supernumerary spines vary in number and are placed between the fourth and the apical fascicles of the tibia. There is one lateral vertical row of setae on those species possessing a false comb (*Jellisonia*) and two lateral vertical rows on those that do not (*Pleochaetoides*). Specialized combs on the metatibia apparently have adaptive significance, since they occur independently in a number of unrelated genera belonging to Leptopsyllidae (*Amphipsylla* Wagner, 1909; *Leptopsylla* Jordan and Rothschild, 1911; *Peromyscopsylla* I. Fox, 1939), Chimaeropsyllidae (*Epirimia* DeMeillon, 1940), and Ischnopsyllidae (*Thaunapsylla* Rothschild, 1907). In every case, there is a reduction in the number of lateral setae when combs are present on the metatibia. Among Ceratophyllidae, tibial combs are exclusive to the subgenus *Jellisonia*. Diagnoses that follow will differentiate only species within the subgenus *Jellisonia*.

Jellisonia (Jellisonia) breviloba breviloba Traub, 1950, new status (Fig. 3B, 5B, 9B, 13B, 16B, 24A)

Jellisonia hayesi breviloba Traub, 1950. Fieldiana: Zoology Memoirs, 1:19, Plate 5. Barrera, 1953:216 [not examined]; Barrera, 1968:71; Muñiz-S. et al., 1981:165 not examined; Ayala-Barajas et al., 1988:68–69; Ponce-Ulloa and Llorente-Bousquets, 1996:558.

Jellisonia hayesi Traub: Tipton and Méndez, 1968:193 [misidentification].

Type Material.—MÉXICO, Michoacán: Mount San Miguel, ex *Microtus mexicanus* (Saussure 1861), 10 May 1933, A. Dampf (holotype male/allotype female) (FMNH).

Diagnosis.—Males of this species are distinguished from other members of the subgenus except *J. breviloba barrerae*, *J. hayesi*, and *J. maxwelli* by the flask-shaped base of the crochet and a loop-like sclerotization intruding inward at the anterodorsal margin of the median dorsal lobe. Males are further separable from *J. hayesi* and

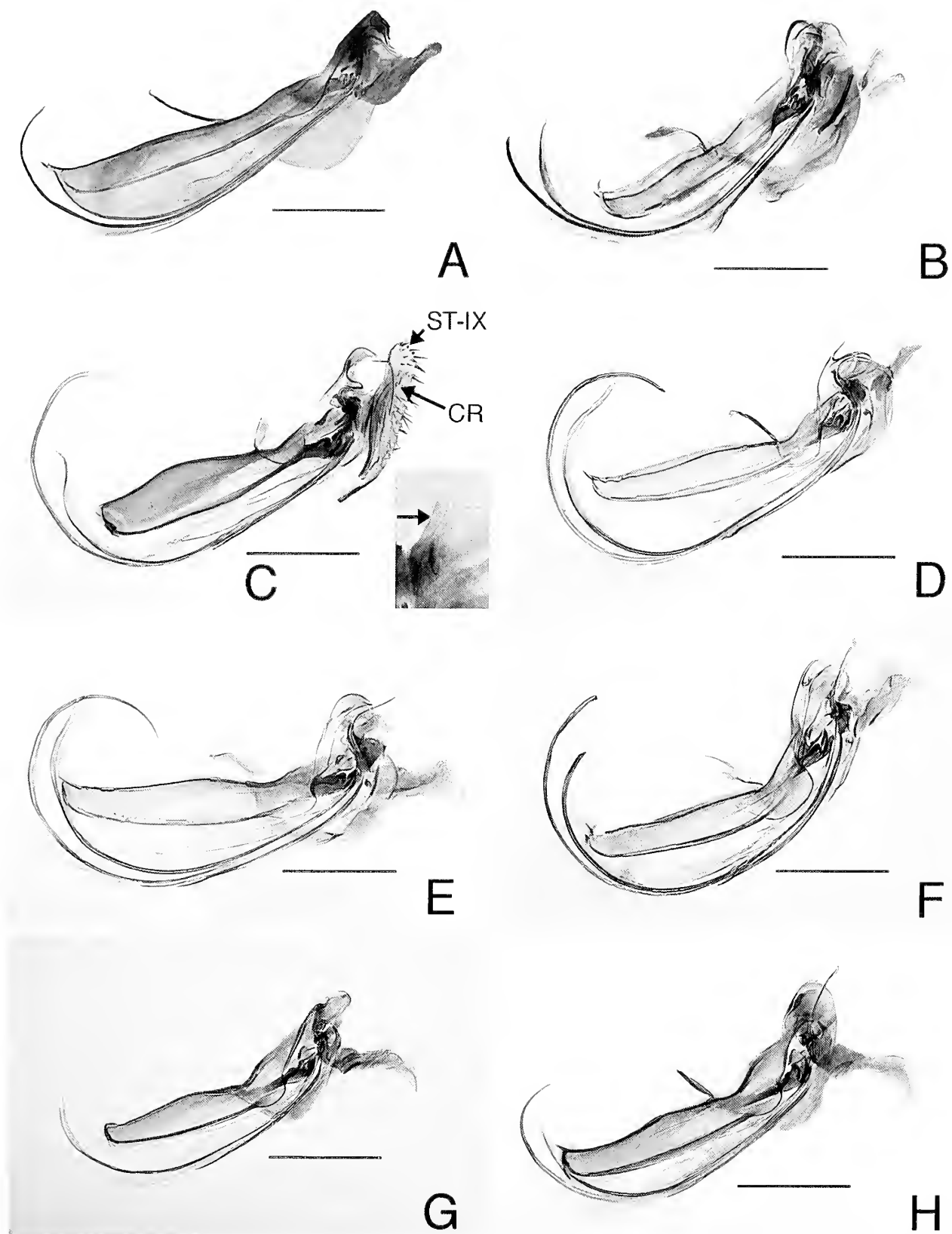


Fig. 4.—Aedeagi of *Jellisonia* species: A, *J. maxwelli*, n. sp.; B, *J. painteri*; C, *J. tiptoni* (enlargement of crochet); D, *J. bullisi*; E, *J. grayi*; F, *J. ironsi*; G, *J. mexicana*; H, *J. wisemani*. (Scale = 200 μm).

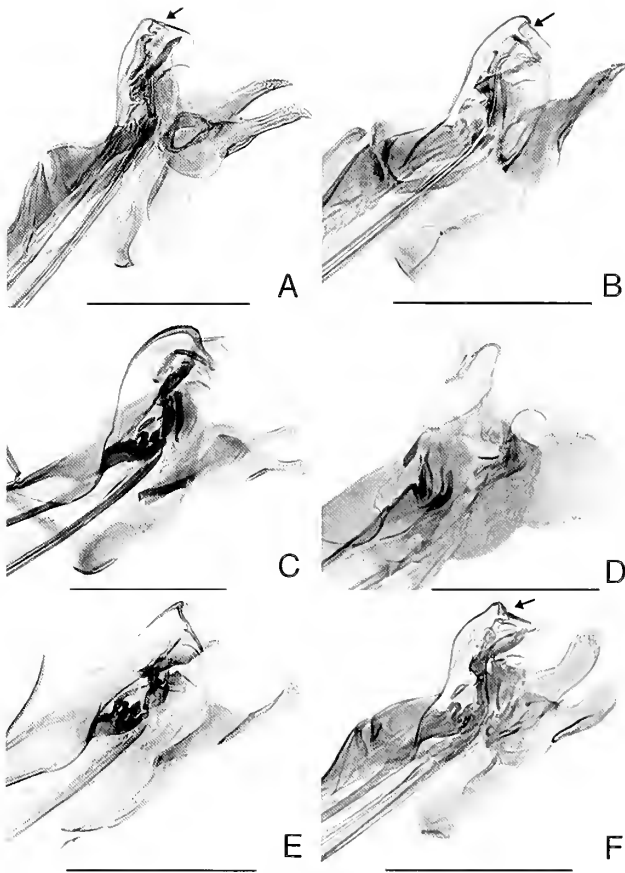


Fig. 5.—Apices of aedeagi in *Jellisonia* species: A, *J. breviloba barrerae*, n. sp.; B, *J. b. breviloba*; C, *J. eckerlini* n. sp.; D, *J. falcata*; E, *J. guerrerensis*; F, *J. hayesi*. Black arrow = loop-like sclerotization; white arrow = vertical sulcus in aedeagal apodeme. (Scale = 200 μ).

J. maxwelli by the conical shape of the apex of the distal arm of sternum IX (broadly rounded and truncate in *J. hayesi* and *J. maxwelli*) and from *J. b. barrerae* by the lack of setae on sternum VIII and without a lobe on the ventrocaudal margin of Ford's sclerite (Fig. 5B). Females are akin to those species whose bursa copulatrix is shorter than the length of the spermatheca and bear three setae on each side of sternites IV–VI (*J. painteri*, *J. hayesi*, *J. maxwelli*, and *J. b. barrerae*). Females are not separable from the latter two species, but differ from the former two taxa by the presence of a small lobe and shallow subtending sinus (Fig. 19C) opposed to a large lobe and deep sinus (Fig. 19A, D).

Material Examined.—**MÉXICO. Coahuila:** La Carbonara, 16 km SE Arteaga, 2075 m, ex *Peromyscus* sp., 2 males, 2 females (CMNH). **Distrito Federal:** "country club," ex *Arvicola mexicana* [= *N. mexicana*], holotype and allotype (FMNH), paratypes (1 male, 1 female) (CMNH); San Andrés, Tetepilco, ex *Microtus mexicanus mexicanus*, 1 male, 1 female (CMNH), 1 male, 5 females (UNAM), 1 female (USNM), 1 male, 8 females (BMNH); Pedregal de San Angel, ex *Peromyscus* sp., 1 female (REL); Cerro Zacayuca, ex *P. truei gratus* [= *P. gratus* Merriam, 1898], 1 female (CMNH), 2 females (BMNH). **Durango:** 16 km W El Salto, ex *Peromyscus* sp., 1 female (CNC), 0.8 km SE Buenos Aires, 2650–2683 m, ex *Peromyscus* sp., 5 males, 3 females (CMNH); 6.5 km S El Salto, ex *Peromyscus* sp., 3 males, 4

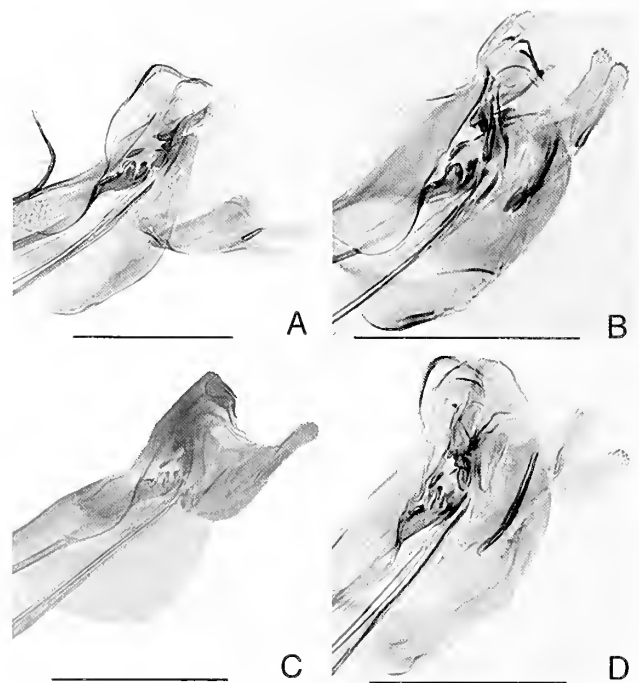


Fig. 6.—Apices of aedeagi in *Jellisonia* species: A, *J. jolmsomae*; B, *J. klotsi*; C, *J. maxwelli*, n. sp.; D, *J. painteri*. (Scale = 200 μ).

females (CMNH); 11 km S El Salto, ex *Peromyscus* sp., 1 male, 1 female (CMNH); 1.6 km SW Revolucioneros, 1982–2043 m, ex *Peromyscus* sp., 8 males, 7 females (CMNH); 8 km E Revolucioneros nr Sinaloa border, 1982 m, ex *Peromyscus* sp., 5 males, 2 females (CMNH); 9.7 km NE Revolucioneros, 2378 m, ex *Peromyscus* sp., 1 male, 2 females (CMNH), 2 females (USNM); 11 km NE Revolucioneros, 2470 m, ex *Peromyscus* sp., 9 males, 5 females (CMNH); 8 km W Revolucioneros nr Sinaloa border, 2012 m, ex *Neotoma* sp., 1 male (CMNH); 3.2 km E Revolucioneros, 11.3 km E Sinaloa border, 2226 m, ex *Peromyscus* sp. 1 male, 2 females (CMNH), ex *Neotoma* sp., 1 male (USNM); 8 km E Revolucioneros, 2012 m, ex *Peromyscus* sp., 1 female, ex *Neotoma* sp., 1 male (USNM); 3.2 km E Revolucioneros, 14.5 km E Sinaloa line, 2348 m, ex *Peromyscus* sp., 2 males, 1 female (CMNH); 4.8 km E Revolucioneros, 12.9 km E Sinaloa line, 2286–2378 m, ex *Peromyscus* sp., 7 males, 3 females (CMNH); 19.4 km E Revolucioneros, 27.4 km E Sinaloa line, 2470 m, ex *Peromyscus* sp., 2 males, 5 females (CMNH); 4.8 km E Revolucioneros nr highway, 14.5 km E Sinaloa line, ex *Peromyscus* sp., 2 females (CMNH); 8 km E Revolucioneros nr Highway, 14.5 E. Sinaloa line, 2348 m, ex *Peromyscus* sp., 2 males, 1 female (CMNH); 48 km W Durango, 2439 m, ex *Peromyscus* sp., 1 male, 1 female (CNC). **México:** 1.8 km N Barrientos, ex *Peromyscus truei* [= (Mexican species equal *Peromyscus gratus*)], 1 male, 2 females (CMNH); 3.2 km N Tlalnepantla, ex *P. truei* [= *P. gratus*], 1 male, 1 female (UNAM). **Guanajuato:** 8 km SW Ibarra, 2500 m, ex *Sigmodon fulviventer* J.A. Allen, 1889, 1 female (CMNH). **Guerrero:** 1.6 km NW Omiltemi, 1912 m, ex *Peromyscus* sp., 2 females (CMNH); Puerto Chico, Camotla las Bravo, ex *Peromyscus banderanus vicinior* [= *Osgoodomys bandaranus* (J.A. Allen 1897)], 1 female (CMNH); and Playa Azul, ex *P. truei* = *P. gratus*, 2 males, 2 females (GML). **Hidalgo:** 12.9 km NE Jacala, 1738 m, ex *Peromyscus lylocetes*? [= *P. aztecus* (Saussure 1860)], 1 female (CMNH). **Jalisco:** Nevado de Colima, nr La Joya, 3354 m, ex *P. lylocetes* [= *P. aztecus*], 1 male, 1 female (CMNH). **México:** 1.8 km N Barrientos, ex *P. truei* [= (Mexican species equal *P. gratus*)], 1 male, 2 females (CMNH); 3.2 km N Tlalnepantla, ex *P. truei* [= *P. gratus*], 1 male, 1 female (UNAM). **Nuevo León:** Cerro Potosí, 2622–3110 m, ex *Peromyscus difficilis* J.A. Allen, 1891, 4 males, 5 females (BYU), 4 males, 5 females (USNM); Cerro Potosí, 2226 m, ex *P. difficilis*, 1 male (CMNH); Cerro Potosí,

2652–3232 m, ex *Peromyscus melanotis* J.A. Allen and Chapman, 1897, 3 females. **Puebla:** 1.6 km NE Alchichicha, 2420 m, ex *Peromyscus maniculatus* Wagner, 1845, 1 male (USNM), 6 males, 12 females (CMNH). **Querétaro:** 2.5 km NW Santa Inés, ex *Peromyscus furvus* J.A. Allen and Chapman, 1897, 2 males, 2 females (UNAM); 2.8 km NW Santa Inés, ex *P. furvus*, 2 males; Maguey Verde, ex *P. difficilis*, 1 male (UNAM). **Sinaloa:** 1 km NE Santa Lucía, 1128 m, ex *Peromyscus boylii spicilegus* [= *Peromyscus spicilegus* J.A. Allen, 1897], 1 male (CMNH); 19.2 km NE Santa Lucía, ex *P. b. spicilegus* [= *P. spicilegus*], 1 male (CMNH); 1.6 km E Pánuco, ex *N. mexicana*, 1 male. **Tamaulipas:** 16.1 km SSW Ciudad Mante, ex *Tadarida femorosacca* [= *Nyctinomops femorosaccus* (Merriam 1889)], 1 female (CMNH). **TLaxcala:** Tlaxco, ex *Peromyscus* sp., 3 males, 2 females (CMNH).

Remarks.—This taxon is elevated to specific status and is no longer considered a subspecies of *J. hayesi* (see Remarks under *J. hayesi*). One male (of 88 specimens) from the state of Durango possessed a single seta on sternum VIII, a character that normally separates this subspecies from *J. b. barrerae*. The sternum VIII of all *J. b. barrerae* examined bore setae and usually two pairs. The specimen from the state of Tamaulipas is the only *Jellisonia* recorded from that state and it was collected from a bat.

Jellisonia (*Jellisonia*) *breviloba barrerae*, new subspecies

(Fig. 3A, 5A, 9A, 13A, 16A, 24B)

Type Material.—**MÉXICO. Distrito Federal:** Meyehualco, 5 km E Santa Cruz, ex *P. difficilis*, 2 males (UNAM); Cerre Zacayuca, *P. truei gratus* [= *P. gratus*], 1 male, 1 female (REL); 21 ? [sic] W Zacatepec, 400 m, ex *P. maniculatus*, 1 male (BMNH). **Morelos:** Lagunas de Zempoala, near Ojo de Agua, 2287 m, ex *P. difficilis*, 1 male, 1 female (CMNH); Derrame Chichinautzin, 2440–2505 m, ex *P. difficilis*, 5 males, 4 females (UNAM), 2470 m, ex *Neotoma mexicana torquata* [= *N. mexicana*], 1 female (UNAM). **Puebla:** 1 km SW San Pedro Atlitxco (18°58'N 98°28'W), 2200 m, ex *P. difficilis*, 22 February 1964, A. Barrera and T. Alvarez, holotype, allotype, and 17 paratypes (7 males, 10 females) (CMNH); 3 males, 5 females (UNAM). Holotype, allotype, and 12 paratypes (4 males, 8 females) deposited in CMNH, 4 paratypes (2 males, 2 females) in USNM, 20 paratypes (10 males, 10 females) in UNAM, 1 paratype (1 male) in BMNH, 2 paratypes (1 male, 1 female) in REL, and 3 paratypes (2 males, 1 female) in the author's collection (MWH).

Diagnosis.—*Jellisonia breviloba barrerae* is most similar to *J. b. breviloba*, *J. hayesi*, and *J. maxwelli* n. sp. (described below). Males are distinguished from those of *J. b. breviloba* and *J. hayesi* by the presence of one or two setae on sternum VIII (Fig. 16A) (setae rare in *J. b. breviloba* and *J. hayesi*) and from *J. maxwelli* by the spiculate, elongate, intersegmental membrane (vestigial in *J. maxwelli*, Fig. 17B). The apex of the median dorsal lobe and shape of Ford's sclerite are also diagnostic for *J. b. barrerae* (Fig. 5A). Female: Among females bearing three setae on each side of sternites IV–VI and having a rather straight bursa copulatrix (not sigmoid-shaped), *J. b. barrerae* is inseparable from the nominate subspecies and *J. maxwelli*; however, it may be separated readily from *J. painteri* and *J. hayesi* by the absence of a distinct lobe subtended by a sinus in the caudal margin of sternum VII (Fig. 19A, 19C–D).

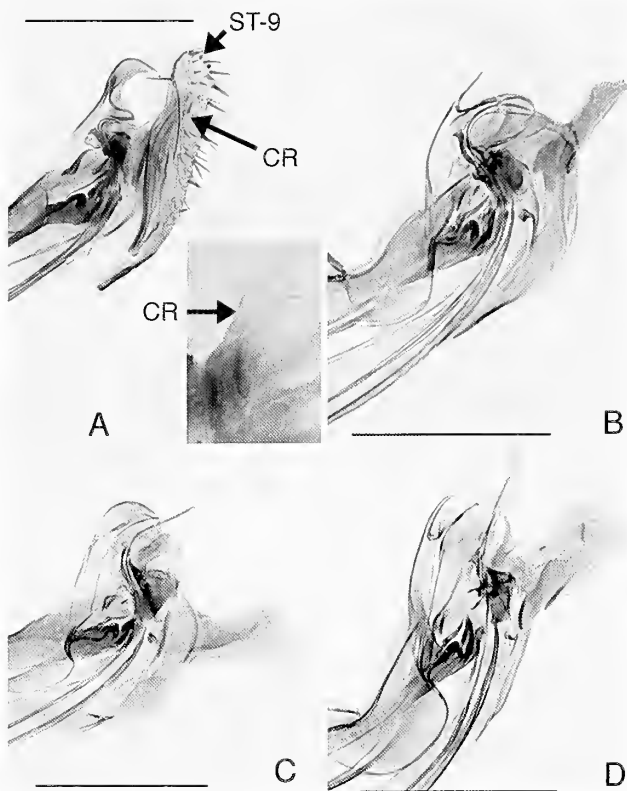


Fig. 7.—Apices of aedeagi in *Jellisonia* species: A, *J. tiptoni* (ST-9=sternum IX, enlargement of CR=crochet); B, *J. bullisi*; C, *J. grayi*; D, *J. ironsi*. (Scale = 200µ).

Description.—**Head.** Preantennal rows with 6, 4, 1 and 3 setae in male; 6, 4, and 3 setae in female. Postantennal rows with 3, 6, and 8 setae on each side; 3, 5, and 6 setae in female. Two setae on each side below oral angle. Fringe of small setae distributed along dorsal margin of antennal fossa. Apical segment of maxillary palpus more than twice length of middle three segments, extending to apex of procoxa. **Thorax.** Pronotum with single row of 7 setae on each side. Mesonotum with 5 setae on each side in main row; mesonotal collar with 4 pseudosetae on each side. Metanotum with 5 setae on each side in main row; 1 marginal spinelet on each side. Metepisternum with 1 long seta. **Legs.** Dorsal margin of each tibia with robust row of setae forming a comb, single lateral row of small setae, mesal row of small setae. **Unmodified Abdominal Segments.** Marginal spinelets on tergites I–IV of male (1, 2, 1, and 1 on each side) and tergites I–III of female (1, 1, and 1 on each side). Male with three antesensorial bristles, lateral and mesal minute, middle large, and borne on sclerotized protuberance; female with three antesensorial bristles, mesal and lateral less than one half length of middle bristle. Female with three setae on each side of sternites III–VI. **Modified Abdominal Segments, male.** Tergum VIII with dorsal fringe of 4–5 setae, dorsolateral group of two setae, ventrolateral group of two setae. Basimere elongate, narrowing towards acetabulum. P1 finger-like; apex at same level as apex of telomere. Telomere with six marginal setae, three spiniform setae grouped at ventrocaudal margin; most ventral much thicker than two adjacent setae. Dorsal setae are slender, not spiniform (Fig. 9A). Apodeme of tergum IX strongly projected cephalad, acutely pointed. Manubrium thick with apex curved upward. Sternum VIII pencil-like; adorned with a single seta on each side; apex with short, forked, membranous extensions less than length of sternite. Intersegmental membrane between sternites VIII and IX spiculate with caudally projected dual plumose extensions (Fig. 16A). Lacking bulbous spiculated intersegmental membrane present in *J. klotsi* (Fig.

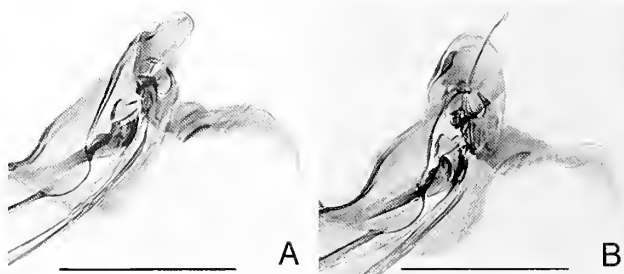


Fig. 8.—Apices of aedeagi in *Jellisonia* species: A, *J. mexicana*; B, *J. wisemani*. (Scale = 200 μ).

17A). Distal arm of sternum IX strongly oblique from ventral inverse seta to apex, anterior margin markedly convex; marked sclerotized protrusion near proximal point of flexure (Fig. 13A). **Aedeagus.** Penis rods just exceeding apex of aedeagal apodeme. Aedeagal apodeme with dorsally expanded hump anterior to narrow neck; hump with vertical sulcus. Dorsal armature heavily sclerotized. Ford's sclerite thickened on caudal margin. Crochet flask-shaped at base, elongate, sharply pointed at apex; apex with tubercles. Paxillus present (Fig. 3A, 5A). **Modified Abdominal Segments, female.** Tergum VIII with 3–5 setae on each side between sensillar plate and tergum VII; dorsal lateral patch of 2–3 setae; ventrolateral patch of 2–3 setae. Caudal margin of sternum VII undulate, without distinct lobes or sinuses; row of 4 lateral setae on each side. Sternum VIII without setae. Bursa copulatrix shorter than length of spermatheca.

Dimensions (slide-mounted specimens).—Average length of males, 2.4 mm, range: 2.2–2.6 mm (n=12). Average

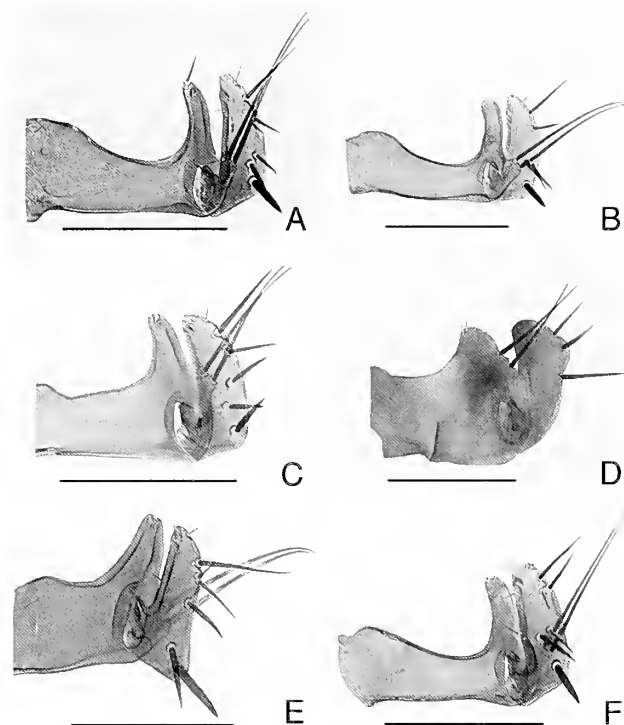


Fig. 9.—Male terga IX of *Jellisonia* species: A, *J. breviloba barrerai*, n. ssp., lateral view; B, *J. b. breviloba*, lateral view; C, *J. eckerlini*, n. sp., lateral view; D, *J. falcata*, lateral view; E, *J. guerrcensis*, mesal view; F, *J. hayesi*, mesal view. (Scale = 200 μ).

length of females, 2.6 mm, range: 2.2–2.9 mm (n=12).

Etymology.—The late Dr. Alfredo Barrera's contributions to our understanding of the flea fauna of Mexico is unparalleled and it is fitting that this new subspecies be named in his honor.

Remarks.—This population of the *J. breviloba* complex has a restricted distribution relative to the nominate subspecies. It may prefer *P. difficilis* as a host, as 38 of 44 specimens (86%) were recorded from that host species. In contrast, of the 24 sympatric specimens of *J. b. breviloba* collected from the Distrito Federal, none were from *P. difficilis* (although one female was from an unspecified species of *Peromyscus*).

Specimens from the states of Morelos and Puebla were conspecific. It should be noted that the anterior margin of the distal arm of sternum IX of males from the Distrito Federal were much more convex than those from Morelos and Puebla, but were similar in other details of the modified segments.

Jellisonia (Jellisonia) eckerlini, new species
(Fig. 3C, 5C, 9C, 13C, 16C, 18A, 22A, 25B)

Type Material.—**COSTA RICA.** **Alajuela:** San Jose (farm of Juan Rafael Cabezz), 1 male, 1 female. **Cartago:** "13 km from end of road at crater," Mount Irazu (~9°58'N 83°51'W), 2590 m, ex *Peromyscus* sp., 26 July 1962, J.T. Creighton, male holotype and 1 male paratype (CMNH); allotype female, same data as holotype except ex *Reithrodontomys* sp., 23 June 1962 (CMNH); the following paratypes with same locality/collector data as holotype but different hosts and collection dates: ex *Reithrodontomys* sp., 26 July 1962, 1 male (CMNH); 23 June/28 July 1962, 2 females (CMNH). ex *Peromyscus* sp., 25 June/16 July 1962, 2 females (CMNH), ex *Scotinomys* sp., 26, 28 July 1962, 3 males, and 3140 m, ex *Reithrodontomys* sp., 22 June 1962, 3 males (CMNH). **Puntarenas:** Cerro Amigos, 1740 m, *Reithrodontomys creper* Bangs, 1902, 7 May 1989, R.M. Timm, 1 male, 1 female (REL). 11 May 1989, R.M. Timm, 1 male (REL); *S. teguina*, 6 May 1989, R.M. Timm, 1 male (REL); Monteverde Cloud Forest Reserve, 1508 m, ex *Oryzomys albigularis* Tomes, 1860, 14 May 1989, R.M. Timm, 1 female (REL); 1580 m, ex *S. teguina*, 17 May 1989, R.M. Timm, 1 male (REL); Monteverde, 1580 m, ex *Peromyscus nudipes* [= *Peromyscus mexicanus* (Saussure 1860)], 30 April 1986, J.S. Ash and R.M. Timm, 1 female (CMNH); 1790 m, ex *Scotinomys* sp., 12 May 1986, J.S. Ash and R.M. Timm, 1 male (CMNH). **San José:** 20 km N San Isidro de General (Pan American Highway), ex *Oryzomys* sp., 1 male (CMNH); 14.5 km N San Isidro de General (Pan American Highway), ex *Oryzomys* sp., 1 female (CMNH); 22.3 km N San Isidro, Cerro Buenavista, ex *Peromyscus* sp., 2 males, 4 females (CMNH); 13 km S Empalme, 2439 m, ex *Peromyscus mexicanus nudipes* [= *P. mexicanus*], 1 male, 1 female (RPE); 14 km SE Empalme, 2500 m, ex *Reithrodontomys* sp., 1 female (RPE); Cerro de la Muerte, 3355 m, ex *P. m. nudipes* [= *P. mexicanus*], 1 male (RPE). Holotype, allotype, and 18 paratypes (8 males, 9 females) deposited in CMNH, three paratypes (2 males, 1 female) in USNM, six paratypes (4 males, 2 females) in REL, four paratypes (3 males, 2 females) in RPE, and two paratypes (2 males, 1 female) in the author's collection (MWH).

Diagnosis.—Male: *Jellisonia eckerlini* may be distinguished from all species in which the crochet is not flask-shaped basally (Fig. 5C), except *J. johnsonae*, by projection of the apex of sternum IX which is bent caudad like a hockey stick (Fig. 13C). It may be separated from *J. johnsonae* by the rounded apical sclerite of the median

dorsal lobe (acutely pointed in *J. johnsonae*) (Fig. 5C, 6A). The posterior margin of the telomere is also convex in *J. eckerlini* and nearly straight in *J. johnsonae* (Fig. 9C, 10A). Females are distinguished from those of other species except *J. johnsonae*, *J. klotsi*, *J. painteri*, and *J. guerrensis* by the absence of a sigmoid-curved bursa copulatrix and the presence of only two setae on each side of sternites IV–VI. The presence of a distinct dorsal lobe on the caudal margin of sternum VII separates *J. eckerlini* (Fig. 18A) from *J. johnsonae* (lobe only indicated, or lacking entirely). The new species differs from *J. klotsi*, *J. painteri*, and *J. guerrensis* by the depth of the sinus on the caudal margin of sternum VII, which is less than the width of dorsal lobe (measured from the greatest depth of the sinus to the closest margin of the dorsal lobe). The deeper sinus in the three species is a reflection of the larger dorsal lobe.

Description.—**Head.** Preantennal area with 3 rows of setae in male (7–8, 4, and 3 on each side); female (5–6, 4, and 3 on each side). Three rows of setae in postantennal area of male (3, 6, and 5 on each side); female (3, 5, and 6 on each side). Female with single long seta behind lowest bristle of main postantennal row. Middle three segments of labial palpus each about half the length of apical segment. Apical segment not extending to apex of coxa. Two setae below oral angle. **Thorax.** Seven setae on each side in single row of pronotum. Nine to 10 spines on each side in pronotal comb. Five setae on each side in main row of mesonotum; 4–5 pseudosetae on each side under mesonotal collar. Six setae on each side in main row of metanotum; each side with single apical spinelet. **Legs.** Mesofemora and metafemora with no lateral setae, a single minute seta on mesal surface. Mesotibiae and Metatibiae with single row of setae on mesal and lateral surfaces; each with false combs on dorsal margins. **Unmodified Abdominal Segments.** Marginal spinelets on tergites I–IV of male (1, 2, 1, and 1 on each side); female tergites I–III (1, 1, and 1 on each side). Female sternum III (3 setae on each side) and sternites IV–VI (2 setae on each side). **Modified Abdominal Segments, male.** Basinere narrowed, extended caudad with P1 and telomere of equal height. Telomere with 5 spiniform setae: two dorsal setae marginal, three ventral setae submarginal. Patch of 12 minute setae on ventrolateral surface of telomere. Pair of acetabular bristles on acetabular projection; dorsal to top of acetabulum (Fig. 9C). Tergum VIII large with dorsolateral and ventrolateral pairs of long setae (both groups of setae are variable); dorsal margin fringed with 3–4 long setae. Sternum VIII vestigial with indication of spiculated intersegmental membrane between sternites VIII and IX (Fig. 16C). Sternum IX shaped like hockey stick with apex markedly bent caudad. Ventral inverse setae set well back from anterior margin of sternum IX. Point of flexure of sternum IX about $\frac{1}{4}$ the distance from juncture of proximal and distal arms to apex of distal arm (Fig. 13C). **Aedeagus.** Aedeagal apodeme without dorsal hump distad to neck. Smooth curved margin of dorsal median lobe distinctly thickened, fused with Ford's sclerite, bluntly rounded at apex. Distal end of lateral lobes membranous, difficult to visualize; anteroventral portion of lateral lobes more sclerotized. Crescent sclerite stubby, thickened in middle. Crochet linear, not flask-shaped at base; caudally directed portion short, apex blunt, studded with tubercles (Fig. 3C, 5C). **Modified Abdominal Segments, female.** Tergum VIII with row of 5 setae on each side near spiracle VIII, dorsolateral group of 2–4 setae; ventrolateral group of 1–2 setae; marginal row of 4 long and 2 short setae; pair of short submarginal setae. Sternum VII with small lobe subtended by shallow sinus, 4–5 lateral setae (Fig. 18A). Sternum VIII without setae. Ventral anal lobe angled, ventrocaudal margin with 3 spiniform setae and 2 slender setae at apex. Bursa cop-

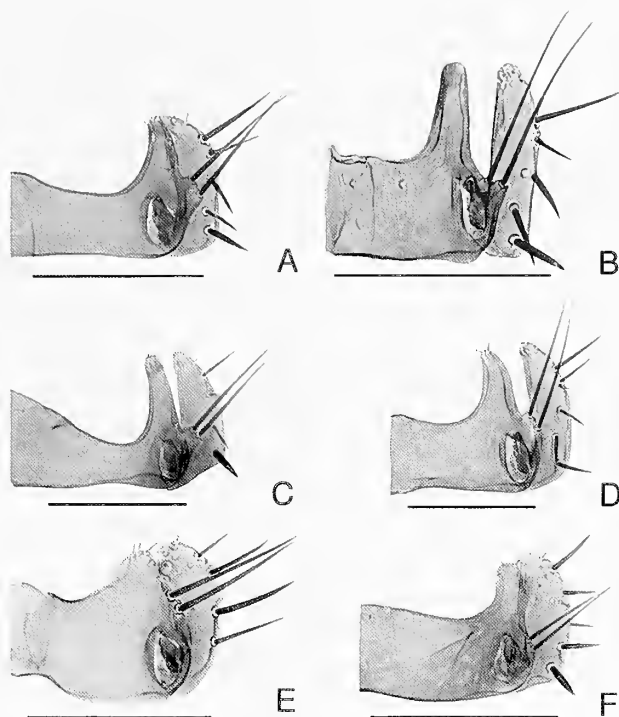


Fig. 10.—Male terga IX of *Jellisonia* species, lateral view: A, *J. johnsonae*; B, *J. klotsi*; C, *J. maxwelli*, n. sp.; D, *J. painteri*; E, *J. tiptoni*; F, *J. amadoi*. (Scale = 200 μ).

ulatrix shorter than length of spermatheca; perula reflexed caudad (Fig. 22A).

Dimensions (slide mounted specimens).—Average length of males, 1.8 mm, range: 1.7–2.1 mm (n=13). Average length of females, 2.4 mm, range: 2.1–2.6 mm (n=8).

Etymology.—This species is named in honor of my friend and colleague, Ralph P. Eckerlin, Northern Virginia Community College, Annandale, Virginia, who has collected fleas extensively in Central America and generously made some of them available for this study.

Remarks.—*Jellisonia eckerlini*, collected at high elevations in the Costa Rican cloud forests of the Cordillera de Talamanca, Cordillera Central, and the Cordillera de Tilarán, has close affinities with *J. johnsonae*. The type locality of *J. johnsonae* is 180 km from the most southeastern record of *J. eckerlini*; however, a few records of *J. johnsonae* are sympatric with the more northern records of *J. eckerlini* in Costa Rica (Fig. 25B). Tipton and Méndez (1966) listed two females from Bocas del Toro and Los Santos Provinces, Panama, and indicated that the dorsal lobe of sternum VII of each was more pronounced than the only species they found in their study (*J. johnsonae*). Although their material could not be located, the pronounced dorsal lobe suggests they might represent *J. eckerlini*, which would tentatively extend the distribution of this new species further south.

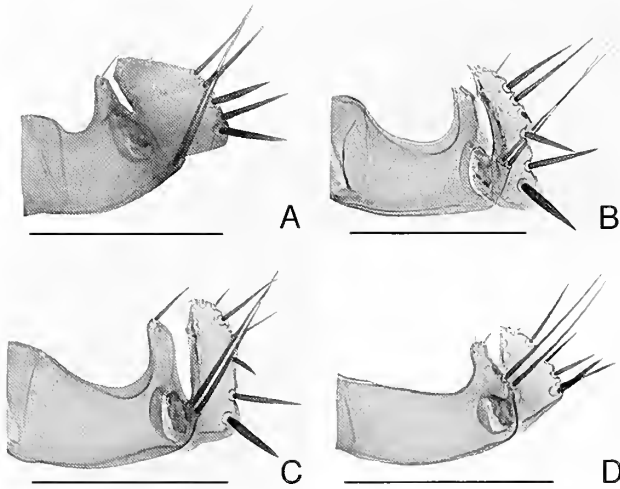


Fig. 11.—Male terga IX of *Jellisonia* species, lateral views: A, *J. bullisi*; B, *J. grayi*; C, *J. ironsi*; D, *J. mexicana*. (Scale = 200 μ).

Jellisonia (Jellisonia) falcata (Méndez and Hanssen 1975), **new combination**
(Fig. 3D, 5D, 9D, 18B, 21D, 25A)

Kohlsia falcata Méndez and Hanssen. 1975. Proceedings of the Entomological Society of Washington, 77:91–96.

Type Material.—**COLOMBIA**. *Meta*: Hacienda “La Conquista,” 70 km N Puerto López, 642 m, ex *Tamandua tetradactyla* (Linn., 1758), July 1971, H. Hanssen (holotype male/allotype female) (USNM No. 73330).

Diagnosis.—Male: *Jellisonia falcata* differs from all other taxa except *J. tiptoni* by the division of the median dorsal lobe into a hook-like dorsal lobe and a secondary ventral lobe, the telomere is broader beyond the middle than at the base, and numerous spiniform setae adorn the distal arm of sternum IX (Fig. 5D, 7A, 9D). There are three marginal setae on the telomere of *J. tiptoni* compared to four on that of *J. falcata* (Fig. 9D, 10E). Females differ from those of *J. tiptoni* by a rounded ventral lobe on sternum VII (acutely sharp in *J. tiptoni*) and from all others by the bursa copulatrix that is sigmoid-shaped and much longer than the spermatheca (Fig. 20A, 21D).

Material Examined.—Holotype and allotype.

Remarks.—This species is transferred from the genus *Kohlsia* to *Jellisonia* based on the following characters unique to *Jellisonia (Jellisonia)*: 1) the presence of false combs on the mesotibiae and metatibiae; 2) the presence of ventral and dorsal inverse setae on the distal arm of sternum IX; 3) the vestigial nature of sternum VIII; 4) the characteristic crochets with tuberculate structures on the apex; 5) lack of a strong (near 90 degrees) anterior flexure of the apex of the bursa copulatrix; and 6) bulga of spermatheca is longer than wide. Méndez and Hanssen (1975) considered *K. fal-*

cata and *K. tiptoni* to be similar species but set apart from all other *Kohlsia* species and with close affinities to *Jellisonia*.

This species is known only from the two males and one female collected from the collared anteater, *T. tetradactyla*. The collared anteater is undoubtedly an accidental host species. This small anteater is largely arboreal, often frequenting the ground and dwelling in earthen or hollow tree cavities previously occupied by other mammals. The opportunity for immature stages of the flea to develop as a result of this host's habits is highly unlikely. Species in this mammalian genus are not known to harbor any host-specific flea species. Although Méndez and Hanssen (1975) suggested an arboreal host, the natural host animal may prove to be a ground-dwelling sigmodontid rodent similar to that of other *Jellisonia* species. The median dorsal lobe of *J. falcata* and *J. tiptoni* is divided into a dorsal falcate lobe and a ventral bluntly rounded lobe. The dorsal falcate lobe was termed the primary median dorsal lobe by Traub (1950) and referenced as such by Méndez and Hanssen (1975). Traub (1950) further defined the more ventral lobe of the median dorsal lobe as the secondary or paradorsal lobe of the aedeagus. These are similar in *J. tiptoni* and have affinities to some species of *Kohlsia*. It should be pointed out that *J. ironsi* and *J. bullisi* also possess these seemingly homologous structures, although they are placed in a different subgenus within this work. Traub (1950) suggested that these structures in the latter two species contribute to a bifurcate aedeagus. Similarities in these four species also include a sclerotized inner tube that is strongly reflexed anteriorly, more so than in other species within the genus *Jellisonia* (a characteristic of *Kohlsia*). *Kohlsia* may ultimately prove to be subordinate to *Jellisonia*.

Jellisonia (Jellisonia) guerrensis Morales, 1990
(Fig. 3E, 5E, 9E, 13D, 16D, 18J–L, 24B)

Jellisonia guerrensis Morales. 1990. The Southwestern Naturalist, 35:310–315. Ponce-Ulloa and Llorente-Bousquets, 1996:558, 564.

Type Material.—**MÉXICO**. **Guerrero**: Agua Fria, 22 km SW Yextla, 2600 m, ex *Peromyscus megalops auritus* [= *P. megalops* Merriam, 1898], 11 April 1963, T. Alvarez (holotype male/allotype female) (UNAM).

Diagnosis.—Males of *J. guerrensis* are associated with those taxa that do not have a bifurcate (divided) median dorsal lobe and lack a loop-like sclerotization intruding inward at the anterodorsal margin of the median dorsal lobe. Included among these are *J. johnsonae*, *J. eckerlini*, *J. painteri*, and *J. klotsi*. Males of *J. guerrensis* are distinct from the former two species by the lack of a caudal projection at the apex of distal arm of sternum IX (Fig. 13C, 14C). *Jellisonia painteri* lacks a concavity in the ventral margin of distal arm of sternum IX, present in *J. klotsi* and *J. guerren-*

sis (Fig. 14A, C). The ventral caudal lobe of the telomere in *J. guerrensis* is much more pronounced than that of *J. klotzi* (Fig. 9E, 10B). Female: The bursa copulatrix is not sigmoid shaped and is similar to those species possessing only two setae on each side of sternites IV–VI. Among these, *J. johnsonae* has no sinus in the caudal margin of sternum VII, *J. eckerlini* has a very broad sinus, and *J. klotzi*, *J. painteri*, and *J. guerrensis* each have a deep sinus (Fig. 18A, 18C–L, 19B, 19D). The latter two taxa are indistinguishable and the separation of *J. klotzi* is uncertain without accompanying males and consideration of geographic locality.

Material Examined.—**MÉXICO.** Chiapas: 17 km NW Teopisca, 1982 m, ex *Peromyscus mexicanus guatemalensis* [= *P. guatemalensis* Merriam, 1898], 1 female (UNAM). Guanajuato: Puerto del Gallo, ex *Oryzomys* sp., 1 male (UNAM). Guerrero: Agua Fria, 22 km SW Yexthla, 2600 m, ex *P. m. auritus* [= *P. megalops*], male holotype, female allotype and 1 female paratype (UNAM); 1.6 km NW Omiltemi, ex *Peromyscus* sp., 1 male paratype (UNAM); Omiltemi, ex *Peromyscus* sp., 3 male paratypes (UNAM); ex *Reithrodontomys* sp., 1 male paratype (UNAM); Puerto Chico, Xochipala, 2600 m, ex *P. m. auritus* [= *P. megalops*], 2 paratypes (1 male, 1 female) (UNAM); Omiltemi, ex *Reithrodontomys* sp., 1 male (UNAM); Chilpancingo, 2.5 km E Omiltemi, ex *P. megalops*, 1 male (UNAM); ex *Megadontomys thomasi* (Merriam 1898), 1 male (UNAM); 4 km N Omiltemi, ex *P. megalops*, 1 male (UNAM); ex *M. thomasi*, 1 female (UNAM); 1.6 km SW Omiltemi, 2012–2013, ex *Peromyscus* sp., 11 males, 2 females (CMNH); 2213 m, ex *Reithrodontomys* sp., 2 males (CMNH); Omiltemi, ex *Peromyscus* sp., 1 male (CMNH); Camotla, Leonardo Bravo, ex *Peromyscus banderanus vicinior* [= *P. banderanus*], 1 male (CMNH). Oaxaca: Tlahuitoltepec, near Santa María Yacochi, 2300–2400 m, ex *Habromys lepturus* (Merriam 1898), 3 males, 1 female, ex *Oryzomys chapmani* Thomas, 1898, 1 female, *P. aztecus*, 1 female, ex *Peromyscus melanocarpus* Osgood, 1904, 2 females (MWH); 7 km SW Suchixtepec, ex *Reithrodontomys* sp., 1 male, ex *Peromyscus* sp., 2 males, 1 female (CMNH); 16 km SW Suchixtepec, ex *Peromyscus* sp., 2 males, 1 female (CMNH); Llano las Flores, 87 km N Oaxaca, ex *Microtus* sp., 1 male, 1 female (CMNH); 1 male, ex *Microtus* nest, 8 males, 12 females, ex *Peromyscus* nest, 1 male, 1 female (CNC). Veracruz: La Joya, ex *Peromyscus* sp., 1 male (CMNH).

Remarks.—Other than “n. sp.” penciled on each slide, the type material received from UNAM had no type designations marked on the slides. Fortunately, it was possible to precisely match the holotype, allotype, and seven of the remaining eight paratypes by comparing the host/locality data in Morales (1990) with data recorded on each of the slides. The last specimen recorded under “Type Data” by Morales (1990) may or may not have been examined in this revision. This slide had the exact data (including “n. sp.” marked on the label in pencil) except for the date: 3 September 1962 versus 2 April 1963. This specimen may represent the last specimen listed by Morales but if so, the date was erroneously recorded under his “Type Data” or on the slide examined.

The ventrocaudal angle of the telomere of *J. guerrensis* is the most pronounced of all *Jellisonia* and the degree of sclerotization is also remarkable. The dorsal lobe of sternum VII of the female is correspondingly large, perhaps a correlation with that of the robust telomere. Although the obscure locality from Veracruz could not be precisely located, it is likely in the southern portion of the state in the mountainous areas associated with Oaxaca. Veracruz is the most eastern limit of the species.

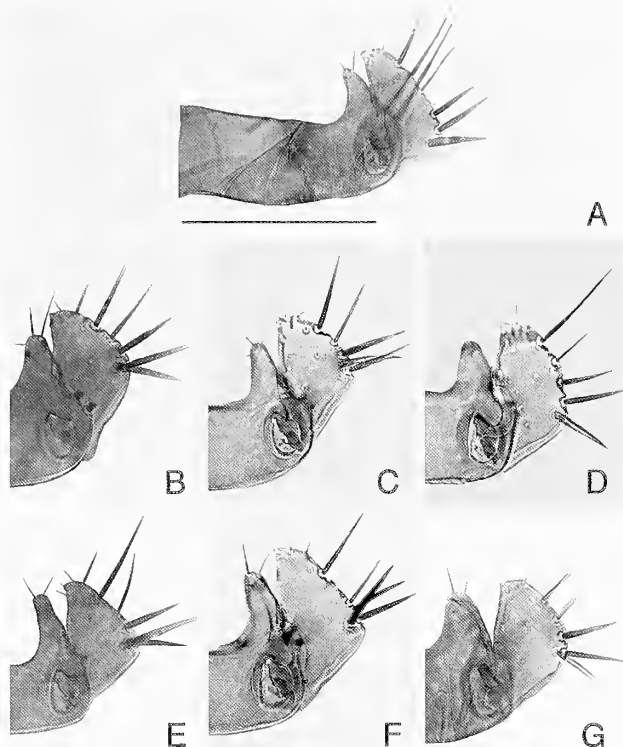


Fig. 12.—Male terga IX of *Jellisonia wisemani*, both antesensorial bristles removed: A, Holotype, *J. wisemani*, Jalisco, México; B, Holotype, *J. bonia*, Veracruz, México (= *J. wisemani*); C, Veracruz, México; D, Jalisco, México; E, Oaxaca, México; F, Chiapas, México; G, Chiquimula, Guatemala. (Scale = 200 μ).

Jellisonia (Jellisonia) hayesi Traub, 1950
(Fig. 3F, 5F, 9F, 13E, 16E, 19A, 22B, 24A)

Jellisonia hayesi hayesi Traub. 1950. Fieldiana: Zoology Memoirs, 1:17–19.

Ayala-Barajas et al., 1988:67–68; Ponce-Ulloa and Llorente-Bousquets, 1996:558.

Jellisonia hayesi Traub: Barrera; 1958:92.

Type Material.—**MÉXICO.** Michoacán: Mount San Miguel, 1982 m, ex *P. hylocetes* [= *P. aztecus*], 30 July 1941, R. Traub, (holotype male/allotype female) (FMNH).

Diagnosis.—Males of *J. hayesi* are distinguished from all species except *J. maxwelli* by the presence of each of the following characters: P1 narrow and finger-like (not broad), median dorsal lobe without a ventral secondary lobe; crochets with a round flask-shaped base (Fig. 5F); and a small lobe on the distal arm of sternum IX anterior to and at the same level as the ventral inverse seta (Fig. 14B). The distal arm of sternum IX differs from that of *J. maxwelli* by the presence of a lobe on the ventral margin and it is rounded at the apex (Fig. 13E). Female: Unlike *J. tiptoni*, the ventral lobe of sternum VII is broadly convex and differs from *J. falcata* by the bursa copulatrix which is subequal in length to the spermatheca and not sigmoid-shaped. It is similar to the two subspecies of *J. breviloba*, *J. maxwelli*, and *J. painteri*. Each has three

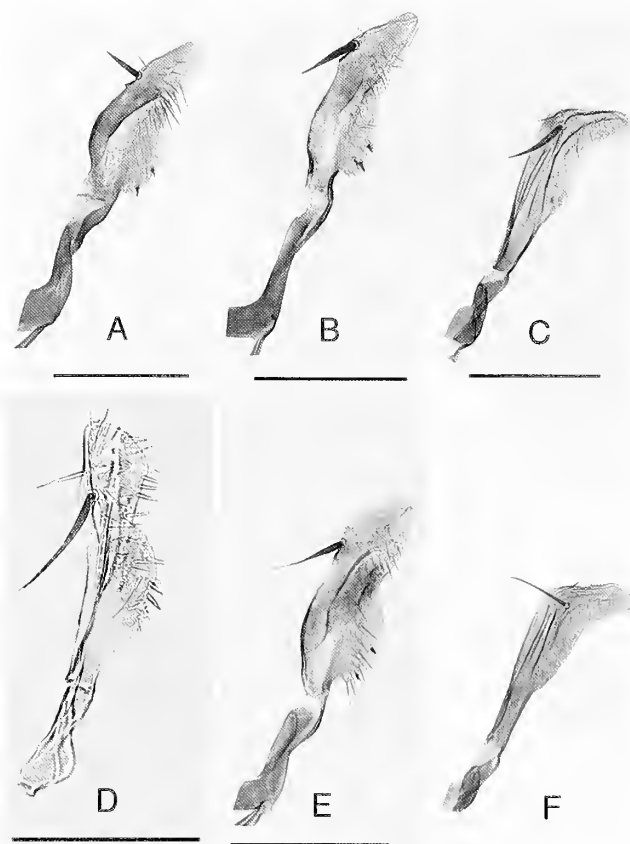


Fig. 13.—Distal arm of male sternum IX in *Jellisonia* species (proximal arm removed): A, *J. brevilooba barrerae*, n. ssp.; B, *J. b. brevilooba*; C, *J. eckerlini*, n. sp.; D, *J. guerrerensis*; E, *J. hayesi*; F, *J. johnsonae*. (Scale = 200 μ).

setae on each side of sternites IV–VI (some *J. painteri* have only two). *Jellisonia hayesi* and *J. painteri* each have a large dorsal lobe and subtending sinus on sternum VII, which is absent in the former three species. In *J. hayesi*, the perula of the bursa copulatrix is not reflected caudad as it is in *J. painteri*.

Material Examined.—**MÉXICO.** **Guerrero:** 1.6 km NW Omiltemi, 2213 m, ex *Peromyscus megalops*?, 1 male (CMNH); 1.6 km SW Omiltemi, 2213–2226 m, ex *Peromyscus* sp., 5 males, 1 female (CMNH); 4.8 km E Omiltemi, 1912 m, ex *Peromyscus* sp., 3 males (CMNH); Camotla, Leonardo Bravo, ex *P. truei gratus* [= *P. gratus*], 1 male, 2 females (CMNH); Omiltemi, ex *Peromyscus* sp., 1 male (CMNH), ex *Liomys* sp., 1 male (CMNH); Chilpancingo, Omiltemi, ex *Peromyscus levipes* Merriam, 1898, 2 males, 1 female, ex *M. thomasi*, 1 male (UNAM); Chichihualco, Camotla, Leonardo Bravo, ex *P. truei* [= *P. gratus*], 1 female (UNAM). **Jalisco:** 1 km S, 19 km W Ciudad Guzmán, 2420 m, ex *Peromyscus* sp., 1 male (CMNH); Nevado de Colima, 2165–3720 m, ex *P. hylocetes* [= *P. aztecus*], 10 males, 8 females (CMNH), 2165 m, ex *Neotoma* sp., 2 males, 3 females (CMNH), 2440 m, ex *Peromyscus* sp., 1 male (CMNH), and 3354 m, ex *Peromyscus* sp., 1 female (CMNH). **Michoacán:** Tancitaro, San Miguel, 1982 m, ex *P. hylocetes* [= *P. aztecus*], holotype, allotype (FMNH) and paratype (1 male) (CMNH); and 10 km S (by road) Pátzcuaro (19°27'35"N, 101°36'27"W), 2200 m, ex *Peromyscus* sp., 1 female (MWH), ex *Baiomys musculus* Merriam, 1892, 1 female (MWH).

Remarks.—Since the original descriptions of *J. h. hayesi* and *J. h. brevilooba*, subsequent collecting has increased the number of known specimens and greatly expanded the distribution of these closely allied taxa. The additional material has enabled a more definitive examination of these previously described subspecies. The structure of the telomere and sternum IX demonstrate the basic differences in *J. hayesi* and the subspecies of *J. brevilooba*. In *J. hayesi*, the apex of the telomere is blunt rather than pointed (Fig. 9A–B, 9F) and the apex of the distal arm of sternum IX is gently rounded instead of straight from the ventral inverse seta to the apex (Fig. 13A–B, 13E). *Jellisonia hayesi brevilooba* is herein elevated to a full species rendering the subspecific status of *J. hayesi* irrelevant. Populations of *J. hayesi* are restricted to the western part of central Mexico at high elevations in Jalisco, Michoacán, and Guerrero, while populations of *J. b. brevilooba* are much more widely distributed from northern Veracruz to Morelos, north to southern Sinaloa, Coahuila, and Nuevo León. The two species are allopatric except for several specimens of *J. b. brevilooba* occurring in Jalisco (1 male, 1 female) and Guerrero (3 males, 6 females). In these sympatric zones, no intergrades of *J. b. brevilooba* and *J. hayesi* have been found.

Variations in several structures were noted in Omiltemi populations from the state of Guerrero. Males do not have an enlarged dorsal hump bearing a short vertical suture on the aedeagal apodeme and the ventrocaudal lobe of the distal arm of sternum IX is less prominent than populations from other states. The Guerrero populations are otherwise conspecific.

Jellisonia (Jellisonia) johnsonae Tipton and Méndez, 1966

(Fig. 3G, 6A, 10A, 13F, 16F, 19B, 22C, 25B)

Jellisonia johnsonae Tipton and Méndez. 1961. Annals of the Entomological Society of America, 54:259–262, pls. 3, 4. Tipton and Méndez, 1966:310.

Type Material.—**PANAMÁ.** **Chiriquí:** Cerro Punta, below Casa Pitty, 1829 m, ex *S. teguina*, 31 January 1960, Keenan and Tipton (holotype male, USNM No. 66653, and allotype female) (USNM).

Diagnosis.—Males of *J. johnsonae* are distinguished from other species except *J. eckerlini* by a combination of the median dorsal lobe lacking a secondary ventral lobe or a loop-like sclerotized intrusion, crochet linear opposed to flask-like (Fig. 6A), and the apex of the distal arm of sternum IX abruptly turned caudad like a hockey stick (Fig. 13F). The apical sclerite of the median dorsal lobe is acutely pointed in *J. johnsonae* (Fig. 6A) and bluntly rounded in *J. eckerlini* (Fig. 5C). Females are similar to other taxa lacking a sinus on the caudal margin of sternum IX but two setae on each side of sternites IV–VI distinguishes *J. johnsonae* from those (Fig. 19B).

Material Examined.—**COSTA RICA.** **Alajuela:** Monteverde Cloud Forest Reserve, 1669 m, ex *P. nudipes* [= *P. mexicanus*], 16 May 1989,

R.M. Timm, 1 female (REL), 1580 m, ex *S. teguina*, 17 May 1989, R.M. Timm, 1 female (REL); 7.4 km S Café la Georgiana, Pan American Highway, ex *Peromyscus* sp., 1 female (CMNH). **San José:** 14 km SE Empalme, 2500 m, ex *P. nudipes* [= *P. mexicanus*], 2 males (RPE); 10 km S Empalme, 2561 m, ex *P. mexicanus*, 1 male, 1 female (RPE).

PANAMÁ. Chiriquí: Bambito, 1524–1768 m, ex “animal nest,” 1 male paratype (BYU), 2 male paratypes (CMNH), ex *P. nudipes* [= *P. mexicanus*], 3 male paratypes, female allotype (USNM), ex *Reithrodontomys mexicanus* (Saussure 1860), 1 female paratype (CMNH), ex *Reithrodontomys sumichrasti* (Saussure 1861), 1 female paratype (CMNH), 2 male, 4 female paratypes (USNM), *S. teguina*, 1 female paratype (BYU), 1 male, 1 female paratypes (USNM); Cerro Barú Cratere, ex *R. sumichrasti*, 1 female paratype (GML); Cerro Punta, 1829–2073 m, *S. teguina*, male holotype, 1 male, 2 female paratypes (USNM), 1 female paratype (BYU), ex *P. nudipes* [= *P. mexicanus*], 1 male paratype (CMNH); Bambito-Cerro Punta, 1524–2134 m, ex *P. nudipes* [= *P. mexicanus*], 1 male (BYU), ex *Reithrodontomys* sp., 1 male (BYU), ex *R. creper*, 1 male (USNM), *R. sumichrasti*, 1 female paratype (BYU), ex *Scotinomys xerampelinus* (Bangs 1902), 1 male (USNM), 1 male, ex *S. teguina*, 3 females (1 paratype) (BMNH), 1 male, 1 female paratypes (BYU), 1 male, 1 female paratypes (CMNH), 1 male paratype (GML), 1 male, 5 female paratypes, 2 male, 3 female (USNM); Lava flow Volcán, *S. teguina*, 1 male (BMNH).

Remarks.—Records of *J. johnsonae* from central Costa Rica are the first reported outside of Panamá. Representatives from Costa Rica are 180 km from records in northern Panama, collected from two of the same host species (*P. mexicanus* and *S. teguina*). This species has been found at 1500–2555 m.

The number of setae in the metatibial comb (below level of last paired setae and excluding the terminal cluster of setae) is rather constant with either four or five single thick setae [five setae on each leg ($n=7$), 4/4 setae ($n=6$), and 4/5 setae ($n=4$)]. One exceptional specimen had four on one side and three on the other. The caudal margin of sternum VII of all females has only a slight indication of a dorsal lobe subtended by a mildly sinuous margin (Fig. 19B). The preferred host (at least in its limited known range) appears to be *S. teguina*.

Jellisonia (Jellisonia) klotsi Traub, 1944

(Fig. 1D, 1G, 3H, 6B, 10B, 14A, 17A, 18C–I, 23B)

Jellisonia klotsi Traub. 1944. Zoological Series of Field Museum of Natural History, 29(15):211–214. Traub, 1950:14–17; Barrera, 1953:215–216; Barrera, 1958:92; Barrera, 1968:71; Ayala-Barajas et al., 1988:69–70; Ponce-Ulloa and Llorente-Bousquets, 1996:558.

Jellisonia dybasi Traub. 1950:19–20. Ponce-Ulloa and Llorente-Bousquets, 1996:558. **New synonymy.**

Type Material.—**MÉXICO. Michoacán:** Cerro Tancitaro, near Tancitaro, ex *Reithrodontomys chrysopsis chrysopsis* = *R. chrysopsis* Merriam, 1900, 12 July 1941, R. Traub (holotype male/allotype female) (FMNH).

Diagnosis.—Male: The characters distinguishing males of *J. klotsi* from other species except *J. painteri* and *J. guerrensis* are the same as those listed below for *J. painteri*. The presence of a deep concavity in the ventral margin of the distal arm of sternum IX characterizes *J. klotsi* and *J. guerrensis* (Fig. 13D, 14A). The lack of a

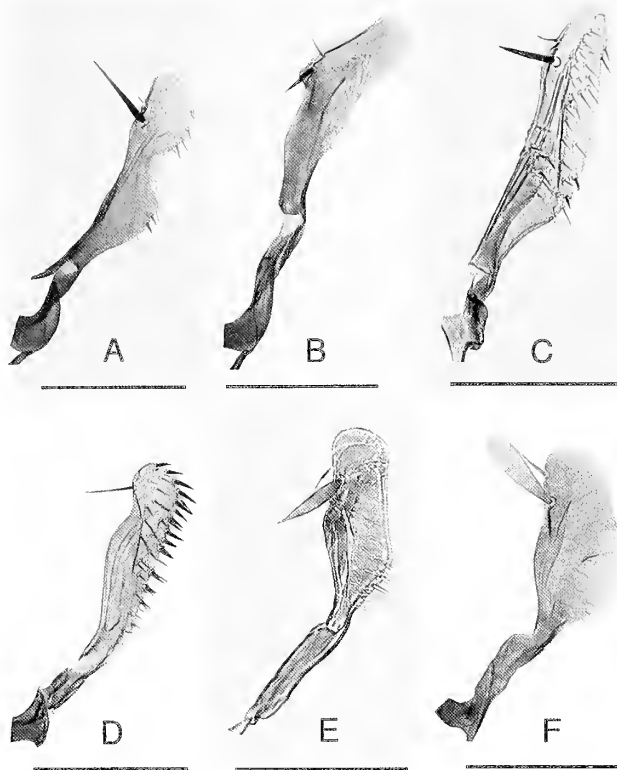


Fig. 14.—Distal arm of male sternum IX in *Jellisonia* species (proximal arm removed): A, *J. klotsi*; B, *J. maxwelli*, n. sp.; C, *J. painteri*; D, *J. tiptoni*; E, *J. bullisi*; F, *J. grayi*. (Scale = 200 μ).

pronounced ventral caudal lobe on the telomere differentiates *J. klotsi* from the latter (Fig. 10B). Female: A deep and narrow sinus in the caudal margin of sternum IX is shared only by females of *J. klotsi* and *J. painteri*. These three species have three setae on each side of sternites IV–VI (some *J. painteri* may have two on each side). Located in Guatemala, females of *J. painteri* with either two or three setae on each side of sternites IV–VI may be separated based on geographical distribution. Without accompanying males, differentiation of *J. klotsi* is uncer-

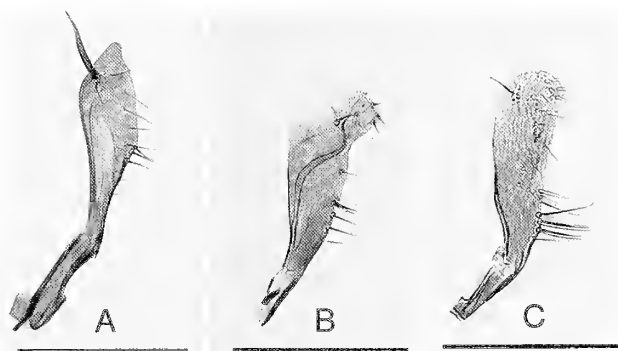


Fig. 15.—Distal arm of male sternum IX in *Jellisonia* species (proximal arm removed): A, *J. ironsi*; B, *J. mexicana*; C, *J. wisemani*. (Scale = 200 μ).

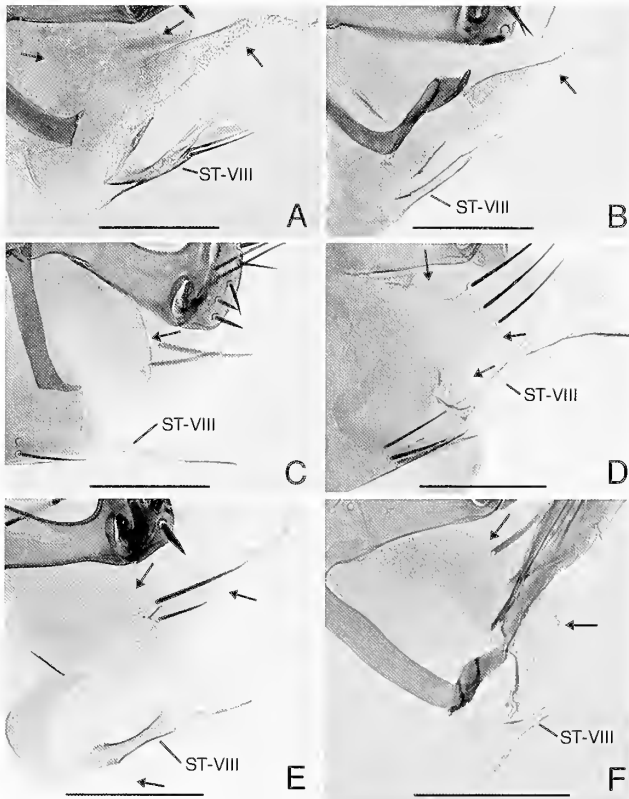


Fig. 16.—Male sternite VIII and intersegmental membranes between sternites VIII (ST-VIII) and IX (black arrows) of *Jellisonia*: A, *J. breviloba barrerae* n. ssp.; B, *J. b. breviloba*; C, *J. eckerlini*, n. sp.; D, *J. guerrensis*; E, *J. hayesi*; F, *J. johnsonae*. (Scale = 200 μ).

tain, but the upper margin of the dorsal lobe of sternum IX tends to be slightly concave in that of *J. klotsi* versus straight to convex in that of *J. guerrensis* (Fig. 18C–I, 18J–K).

Material Examined.—**MÉXICO.** **Distrito Federal:** 42 km N Cuernavaca [Cuernavaca], ex *P. lylocetes* [= *P. aztecus*], 1 female (UNAM); 5 km SW Parres, 3000 m, ex *Reithrodontomys* sp., 2 males, 1 female (UNAM); 3100 m, ex *Neotomodon alstoni alstoni* [= *N. alstoni* Merriam, 1898], 1 female (UNAM); **Jalisco:** Nevado de Colima, 3323–3354 m, ex *P. melanotis*, 2 males, 1 female (UNAM), 3201–3354 m, ex *Microtus* sp., 3 males, 2 females (CMNH), ex *M. mexicanus*, 1 male, 1 female (CMNH), ex *P. lylocetes* [= *P. aztecus*], 1 male (CMNH), ex *P. melanotis*, 5 males, 3 females (CMNH), ex *Peromyscus* sp., 2 males, 3 females (CMNH), ex *Reithrodontomys* sp., 7 males, 6 females (CMNH). **México:** Lagunas de Zempoala, near Ojotongo, 2743–2774 m, ex *P. maniculatus*, 5 males, 1 female (CMNH); 2790 m, ex *Peromyscus* sp., 3 males, 3 females (CMNH); Río Frio, Llano Grande, 3200 m, ex *N. alstoni*, 2 females (CMNH); 4 km W Río Frio, 3000 m, ex *N. alstoni*, 1 female (CMNH). **Michoacán:** Tancitaro, Mt. Tancitaro, 2380 m, ex *Reithrodontomys* sp., 1 male holotype, 2440 m, 1 female allotype (FMNH), 2380–2440 m, ex *R. c. chrysopsis*, 1 male, 1 female paratypes (BMNH), 1 male paratype, ex *Reithrodontomys* sp., 2 male, 2 female paratypes (CMNH), 2 male, 2 female paratypes (USNM). **Morelos:** Lagunas de Zempoala, near Ojotongo, 2590 m, ex *Reithrodontomys* sp., 1 female (CMNH); Lagunas de Zempoala, near Ojo de Agua, 2287 m, ex *Neotomodon* sp., 1 male (CMNH), ex *P. difficilis*?, 1 male (CMNH). **Puebla:** Popocatepetl, ex *Reithrodontomys* sp., 1 female (UNAM), 3100 m, ex *Reithrodontomys* sp., 1 female (CMNH). **Tlaxcala:** 10 km NE Calpulápan [Calpulápan], 3100 m,

ex *Reithrodontomys* sp., 1 male (UNAM). **Veracruz:** Acajete, ex “rodent nest under rock in field,” 30 July 1941, H. Dybas, (*J. dybasi* female holotype) (FMNH).

Remarks.—The caudal margin of sternum VII has a strong lobe subtended by a deep sinus; however, variation in the caudal margin occurs even within the same population (Fig. 18C–H). These features are indistinguishable from those of *J. dybasi* (Fig. 18I), while the dorsal margin of the lobe of *J. guerrensis* tends to be more convex (Fig. 18J–L).

Jellisonia dybasi was described from one female and no additional specimens have since been reported. Traub (1950) considered *J. dybasi* to have close affinities with *J. klotsi* and reported differences in the shape of the caudal margin of the sternum VII and the number of lateral setae, the number of submedian setae of tergum VIII, the number of setae on the mesepimeron, and relative lengths of mesothoracic tarsal segments I and III. Females of *J. guerrensis* are also similar to those of *J. dybasi* and *J. klotsi*. Series of *J. klotsi* and *J. guerrensis* were studied and the characters listed by Traub proved to be quite variable from the same locality or even from opposite sides of the same flea. For *J. dybasi*, these characters fall within the ranges of these variations. Records of *J. klotsi* are restricted to a narrow zone of 19–20 degrees north latitude from the western Pacific coastal state of Jalisco to the eastern Caribbean coastal state of Veracruz. The distribution of *J. guerrensis* occurs below 18 degrees north latitude. *Jellisonia dybasi* falls within the known distribution of *J. klotsi* and not that of *J. guerrensis*. In addition, the dorsal lobe of sternum VII is narrow, slightly concave dorsally, and the ventral lobe extends beyond the apex of the dorsal lobe in *J. klotsi* and *J. dybasi*. The dorsal lobe of *J. guerrensis* is wider, convex dorsally, and the ventral lobe hardly extends beyond the apex of dorsal lobe. This evidence suggests that *J. dybasi* is a junior synonym of *J. klotsi*, representing an extreme eastern limit of *J. klotsi*.

Jellisonia (Jellisonia) maxwelli, new species
(Fig. 4A, 6C, 10C, 14B, 17B, 19C, 22D, 24B)

Type Material.—**MÉXICO.** Nuevo León: Chipinque (25°55'N, 100°23'W), 1310–1463 m, ex *Peromyscus* sp., 26–27 August 1965, J. O'Keefe and R. Kronmeyer. Holotype male, allotype female, and 5 female paratypes deposited in CMNH.

Diagnosis.—This new species is similar to *J. hayesi* and the two subspecies of *J. breviloba*. Male: The crochet has a round flask-shaped base and the median dorsal lobe has a loop-like sclerotized intrusion on the anterodorsal margin (Fig. 4A, 6C). The most ventral seta of the telomere is especially stout in contrast to the four more dorsal marginals that are slender and not spiniform (Fig. 10C). Two or more of the marginal setae are spiniform in *J. hayesi* and the subspecies of *J. breviloba*. Further distinguished from *J. hayesi* and *J. b. breviloba* by the presence of one

or two setae on sternum VIII (Fig. 17B) and from *J. b. barrerai* by the truncate apex of the sternum IX (Fig. 13A, 14B) and the lack of an elongate and spiculated intersegmental membrane (Fig. 16A, 17B). Females are separated from those of *J. hayesi* by the absence of a large dorsal lobe on the caudal margin of sternum VII (Fig. 19A, 19C), while indistinguishable from both subspecies of *J. breviloaba*.

Description.—**Head.** Preantennal area with 3 rows of setae in male (7–8, 4, and 3 on each side); female (7–8, 4, and 3 on each side). Three rows of setae in postantennal area of male (3, 5, and 7 on each side); female (3, 6, and 6 on each side). Other features of head indistinguishable from those of *J. eckerlini*. **Thorax.** Pronotum with single row of 6 setae on each side, otherwise thorax indistinguishable from *J. eckerlini*. **Legs.** Fifth tarsal segment of each leg with 2 preapical plantar bristles; these of fore and mesothoracic legs more spiniform than those of metathoracic leg, stouter in male than female. **Unmodified Abdominal Segments.** Spinelets of tergites I–IV (1, 2, 1, 1 on each side, respectively). Female sternites III–VI, each with row of 3 setae on each side. **Modified Abdominal Segments, male.** Dorsocaudal margin of tergum VIII a smoothly rounded right angle; without setae. Dorsal margin with 3–4 slender setae and 2 larger setae; anterolateral group of 2–3 setae; ventrolateral group of 2–3 setae. Basimere elongate, neck-like with P1 narrow, height equal to apex of telomere. Two acetabular bristles borne on projection. Telomere distinctly tapered base to apex; adorned with single thick heavily pigmented spiniform seta and 4 slender marginal setae, all on mesal surface (Fig. 10C). Sternum VIII slender, pencil-like with single seta on each side; apex beyond setae with bifurcate membranous extension with unique shape (Fig. 17B). Intersegmental membrane with bulbous extension protruding caudad between distal arms of sternum IX. Distal arm of sternum IX divided into proximal sclerotized basal portion and distal enlarged structure, each separated by a flexure point. Distal portion narrow near point of flexure; widening toward ventral inverse seta. Inverse setae both set back from margin with a distinct lobe anterior to each. Portion dorsal to inverse setae extending oblique to bluntly rounded apex. Lateral patch of many short, fine setae on enlarged portion of sternum IX (Fig. 14B). **Aedeagus.** Median dorsal lobe with sclerotized thickening along dorsal margin; loop-like intrusion as it turns caudad. Lateral lobe small near apex; enlarging ventrally. **Modified Abdominal Segments, female.** Tergum VIII with 4 setae along caudal margin; 2 short mesal setae anterior to margin. Tergum VIII with dorsolateral patch of 3–4 setae, ventrolateral patch of 2–3 setae on tergum VIII. Ventrocaudal margin of ventral anal lobe as broad as length of lobe. Anal stylet with long apical seta, ventrolateral medium length seta, one dorsal minute seta at base of apical seta. Main row of sternum VII with 5–6 long setae; caudal margin undulate (Fig. 19C). Bursa copulatrix about same length as spermatheca (Fig. 22D).

Dimensions (slide mounted specimens).—Male, 2.1 mm (n=1); average length of females, 2.5 mm, range: 2.4–2.8 mm (n=6).

Etymology.—This species is named in honor of Taylor J. Maxwell, friend, colleague, and graduate student, who unselfishly collected fleas in Oaxaca, Mexico, during mammalogy studies conducted by Dr. Duke R. Rogers, Brigham Young University. Mr. Maxwell generously provided these specimens to the author for study. The inability to classify his material with current literature was a major catalyst for embarking upon this revision.

Remarks.—Field notes indicate this small series was collected in “mesa, pine, oak forest, rocks.” Associations with other flea species included several specimens of *Epitedia wenmanni* (Rothschild 1904), an unidentified species of *Peromyscopsylla* I. Fox, 1939, and *J. bullisi* (2 males, 1 female).

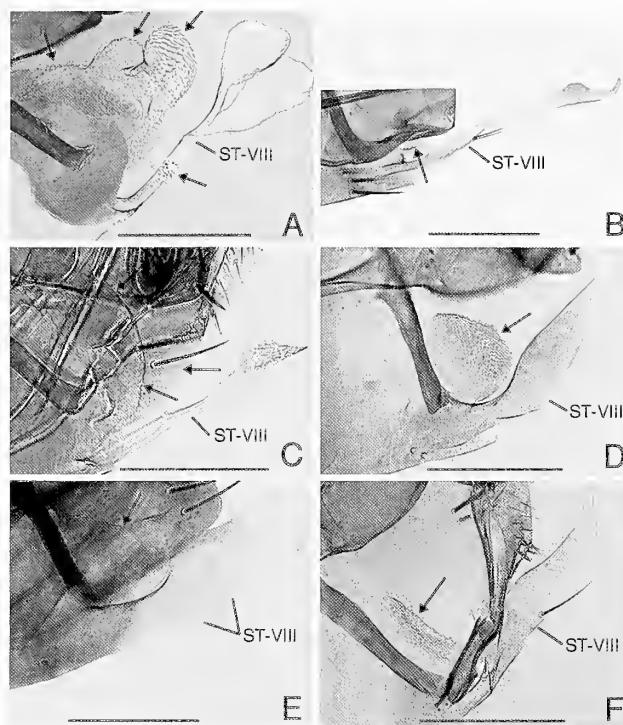


Fig. 17.—Male sterna VIII and intersegmental membranes between sternites VIII (ST-VIII) and IX (black arrows) of *Jellisonia*: A, *J. klotsi*; B, *J. maxwelli* n. sp.; C, *J. painteri*; D, *J. bullisi*; E, *J. grayi*; F, *J. ironi*. (Scale = 200µ).

Jellisonia (Jellisonia) painteri Hastriter and Eckerlin, 2003

(Fig. 2A–E, 4B, 6D, 10D, 14C, 17C, 19D, 22E, 25B)

Jellisonia painteri. Hastriter and Eckerlin. 2003. *Annals of Carnegie Museum*, 72:215–221.

Type Material.—**GUATEMALA. Zacapa:** Río Hondo, Sierra de las Minas, 6 km NNW San Lorenzo (15°08'26"N, 89°40'36"W), 2200 m, ex *Habromys lophurus* (Osgood 1904), 12 April 1998, R.P. Eckerlin (holotype male) (USNM).

Diagnosis.—Males of *J. painteri* are separable from all species except *J. klotsi* and *J. guerrensis* by the following combination of characters: median dorsal lobe without a secondary ventral lobe or a loop-like sclerotized intrusion; crochet linear opposed to flask-like (Fig. 6D); the apex of the distal arm of sternum IX does not project caudad. The lack of a concavity on the ventral margin of distal arm of sternum IX differentiates it from *J. klotsi* and *J. guerrensis* (Fig. 14C). For a detailed diagnosis of *J. painteri* females, see Hastriter and Eckerlin (2003).

Material Examined.—**GUATEMALA. Baja Verapaz:** Finca la Union (15°12'N, 90°12'W), ex *Nyctomys sumichrasti* (Saussure 1860), 1 female (MWH). **Zacapa:** Río Hondo, Sierra de las Minas, 6 km N San Lorenzo (15°08'26"N, 89°40'36"W), 2200 m, ex *H. lophurus*, male holotype and 6 male, 12 female paratypes, ex *Peromyscus grandis* Goodwin, 1932, female allotype and 5 male paratypes, ex *Reithrodontomys microdon* Merriam, 1901, 1 male, 1 female paratypes (for repositories of type material see distribution Hastriter and Eckerlin 2003:216).

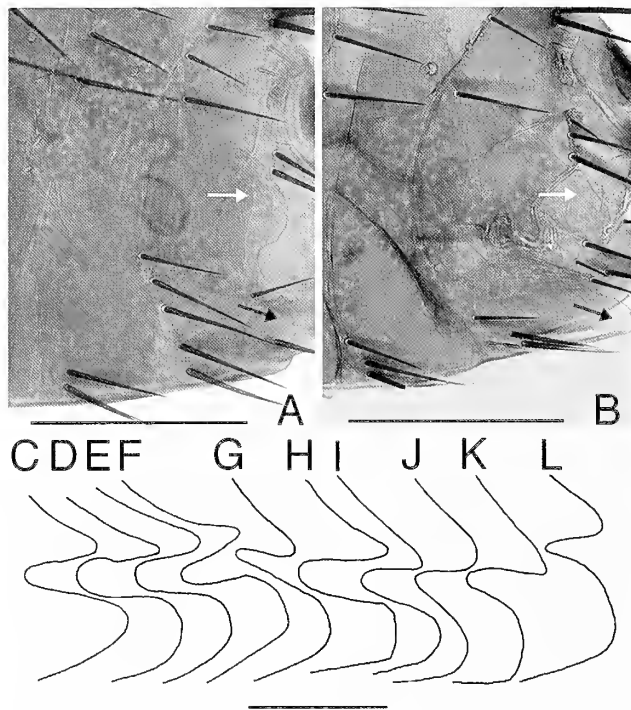


Fig. 18.—Female sternal features of *Jellisonia* species: A–B, Female sternites VI and VII of *Jellisonia* species (white and black arrows = dorsal and ventral lobes of sternum VII, respectively); A, *J. eckerlini* n. sp. (paratype); B, *J. falcata* (allotype); C–L, caudal margin of female sternite VII: C–E, *J. klotsi*, Jalisco, Nevado de Colima; F, *J. klotsi*, Distrito Federal, 5 km SW Parres; G, *J. klotsi*, Estado de México, Lagunas de Zempoala; H, *J. klotsi*, Estado de México, Río Frio, Llano Grande; I, *J. dybasi*, holotype, Veracruz, Acajete (= *J. klotsi*); J–K, *J. guerrensis*, Oaxaca, Santa María Yacochi; L, *J. guerrensis*, allotype, Agua Fria, 22 km SW Yextla. (Scale = 200 μ).

Remarks.—Hastriter and Eckerlin (2003) proposed *H. lophurus* and *P. grandis* as the preferred hosts for *J. painteri*. Wilson and Reeder (1993) indicated that *P. grandis* occurs in the southern part of Alta Verapaz Department and through northeastern Baja Verapaz Department, Guatemala, while *H. lophurus* has a broader distribution from the highlands of Chiapas, Mexico, to central Guatemala and northwestern El Salvador. The known distribution of this flea is limited to the departments of Zacapa and Baja Verapaz. It probably follows the distribution of its preferred host species and may occur in montane habitats of southwestern Mexico, Guatemala, El Salvador, and possibly northwestern Honduras. Additional collecting, especially from *H. lophurus*, is required to further clarify the distribution of this flea.

Jellisonia (Jellisonia) tiptoni (Méndez and Altman, 1960), **new combination**
(Fig. 4C, 7A, 10E, 14D, 20A, 22F, 25A)

Kohlsia tiptoni Méndez and Altman. 1960. Proceedings of the Entomological Society of Washington, 62:45–50.

Type Locality.—PANAMA. Panamá: Cerro Azul [= Cerro Prominente], ex *Didelphis marsupialis* Linnaeus, 1758, 29 January 1958, MCF-PMS, (holotype male, USNM No. 65493),

and ex *Tylomys panamensis* (Gray 1873) (allotype female) (USNM).

Diagnosis.—Male: As in *J. falcata*, this taxon differs from all other members of the subgenus by the bifurcate median dorsal lobe, shape of the telomere, and details of the distal arm of sternum IX (Fig. 5D, 7A, 9D). There are four marginal setae on the telomere of *J. tiptoni* compared to three on that of *J. falcata* (Fig. 9D, 10E). Female: Only *J. tiptoni* and *J. falcata* have a sigmoid-shaped bursa copulatrix (much longer than the spermatheca) but *J. tiptoni* differs from *J. falcata* by the acutely sharp ventral lobe of sternum VII (Fig. 18B, 20A).

Material Examined.—COSTA RICA. Puntarenas: Monteverde, Río Guacimal, ex *N. stanichrasti*, 1 female (CMNH).

GUATEMALA. Izabal: Cerro San Gil las Torres, 915 m, ex *N. sumichrasti*, 14 June 1994, R.P. Eckerlin, 6 males, 2 females (RPE); Cerro San Gil las Brisas, ex *N. sumichrasti*, 29 June 1994, G.E. Meier, 1 female (RPE); and Cerro Poso de Agua, Mpio. Morales, ex *Tylomys nudicaudatus* [= *Tylomys nudicaudus* (Peters 1866)], 10 July 1994, G.E. Meier, 1 female (RPE).

HONDURAS. Lempira: Parque Nacional Celaque Don Tomás, 2083m, ex *P. mexicanus*, 13 February 1998, R.P. Eckerlin, 1 male (RPE).

NICARAGUA. Matagalpa: Santa María de Ostuma, 1250m, ex *Peromyscus mexicanus saxatilis* [= *P. mexicanus*], 3 July 1967, J.D. Smith, 1 female (CMNH).

PANAMA. See holotype and allotype (USNM).

Remarks.—*Kohlsia tiptoni* is transferred to the genus *Jellisonia* based on the same rationale as discussed in the Remarks section of *J. falcata*. It is noteworthy that these two closely related species both comprise the most southern distribution of the genus. The primary hosts are peromyscine rodents with the exception of several records of the semi-arboreal hosts *T. panamensis* and *T. nudicaudus* that are likely accidental associations.

Subgenus *Pleochaetoides* Augustson, 1944, **new status**

Type Species: *Pleochaetoides bullisi* Augustson. 1944. Journal of Parasitology, 30:366–368 (USNM No. 57189) (by monotypy).

Diagnosis.—The absence of a false comb on the dorsal margin of the metatibia is diagnostic for the subgenus. See details in diagnosis of the subgenus *Jellisonia* above. Diagnoses that follow will differentiate only species within the subgenus *Pleochaetoides*.

Jellisonia (Pleochaetoides) amadoi Ponce-Ulloa, 1989,
new subgeneric combination
(Fig. 2F, 10F, 24A)

Jellisonia amadoi Ponce-Ulloa. 1988. Folia Entomológica Mexicana, 76:179–181, figures 1A–C. Ponce-Ulloa and Llorente-Bousquets, 1996:558, 564.

Type Material.—MÉXICO. Guerrero: El Faisanal, 1140 m, Sierra de Atoyac de Álvarez, ex *P. megalops*, 29 October 1983, HP/JJG (holotype male) (UNAM).

Diagnosis.—Females are unknown, and males are distin-

guished from all other taxa within the genus by the "mane" of setae projecting perpendicular to the surface of the mesonotum, metanotum, and tergum I (Fig. 2F).

Material Examined.—**MÉXICO.** Guerrero: La Golondrina, Atoyac, 1750 m, ex *P. megalops*, 003 HP/560 JJG, 1 male paratype (UNAM).

Remarks.—Only the original type series of 11 males is known. Since the author was unable to examine all of the specimens, it is of value to present a summary of the data presented by Ponce-Ulloa (1988). Six of the 11 specimens were collected from *P. megalops* (1140–1750 m), two from *P. aztecus* (900 and 1400 m), two from *Oryzomys alfaroni* = *O. alfaroi* (J.A. Allen 1891) (1400 and 1550 m), and one from *N. mexicana* (1140 m). It is peculiar that the female was not collected considering the variety of hosts and apparent differences in elevations from which the type series was collected.

Jellisonia amadoi has several morphological features that are unique. The dorsal setae on the mesonotum, metanotum, and tergum I are fine and extend dorsad [similar to the mane of some other fleas, e.g., males of *Opisodasys pseudarctomys* (Baker 1904) and *Opisodasys vespertalis* (Jordan 1929)] as opposed to lying flat against the cuticle. The setae on apices of the first three segments of the hind tarsi are also extra long and slender. Several setae on each of these segments extend the length of the next two segments. Although the author did not examine specimens of *J. amadoi* in the UNAM collection, these two features were reportedly present in specimens deposited at UNAM (personal communication, Juan J. Morrone, UNAM).

Jellisonia (Pleochaetoides) bullisi (Augustson 1944)
(Fig. 1E, 4D, 7B, 11A, 14E, 17D, 20B, 21C, 23A)

Pleochaetoides bullisi Augustson, 1944. Journal of Parasitology, 30:366–368.

Jellisonia bullisi (Augustson): Traub, 1950:21–23; Eads, 1950:38–39; Ayala-Barajas et al., 1988:67; Ponce-Ulloa and Llorente-Bousquets, 1996:558.

Type Material.—**UNITED STATES OF AMERICA. TEXAS. Bexar Co.:** Camp Bullis, ex *Peromyscus pectoralis laceianus* [= *Peromyscus pectoralis* Osgood, 1904], 1 June 1944, Augustson (male holotype, USNM No. 57189). Traub later "designated" a female allotype with the following data appearing on the label: "Det. Traub 1950. Desig. Allotype"/"No. 700, Host: mouse, State: Nuevo León, Municip'y: Sabinas Hidalgo, V 1940, K.L. Knight" (FMNH).

Diagnosis.—Males of *J. bullisi* are similar to *J. ironsi* by the presence of a bifurcate median dorsal lobe (Fig. 7C–D), while they are distinguished by the number of dorsal notches in the metatibia (nine in *J. bullisi* and eight in *J. ironsi*). Female: Taxa that have only one seta in the penultimate dorsal notch (counting from proximal) include *J. bullisi* and *J. grayi*. The latter has two lobes on the caudal margin of sternum VII, while *J. bullisi* lacks a dorsal lobe and has a protruding ventral lobe (Fig. 20B).

Material Examined.—**MÉXICO. Nuevo León:** Sabinas Hidalgo, ex "mouse," female allotype (FMNH), 2 males, 1 female (BMNH), 3 males,

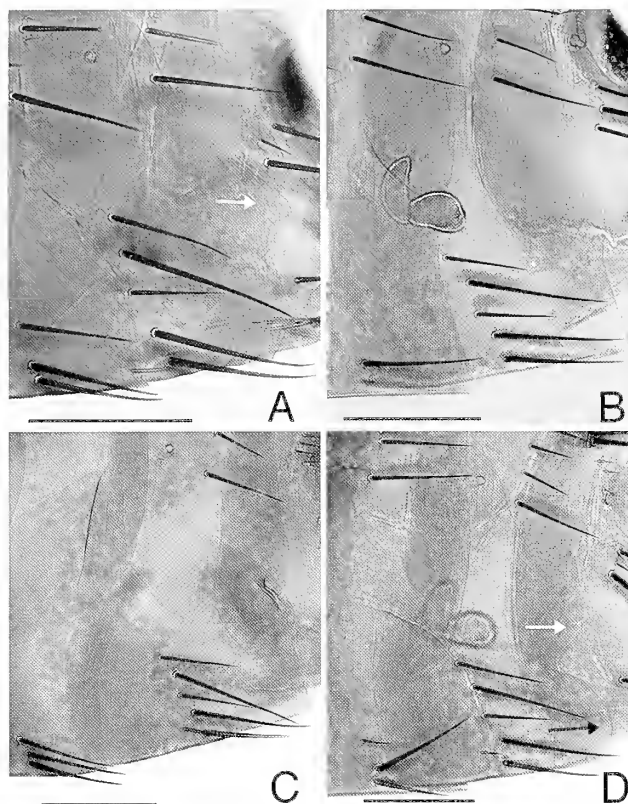


Fig. 19.—Female sternites VI and VII of *Jellisonia* species (white and black arrows = dorsal and ventral lobes of sternum VII, respectively): A, *J. hayesi*; B, *J. johnsonae* (paratype); C, *J. maxwelli* n. sp. (paratype); D, *J. painteri* (paratype). (Scale = 200µ).

1 female; Cola de Caballo, Barrancas, ex *Peromyscus* sp., 1 male (UNAM); 4 km SE Monterrey, ex *Peromyscus* sp., 2 males, 3 females (UNAM); Chipinque, 1311 m, ex *Peromyscus* sp., 2 males, 1 female (UNAM).

UNITED STATES OF AMERICA. TEXAS. Bexar Co.: Camp Bullis, ex *P. p. laceianus* [= *P. pectoralis*], male holotype (USNM). **Kinney Co.:** Kickapoo Cavern State Park, ex *P. pectoralis*, 3 male, 4 female (REL). **Martin Co.:** ex *Perognathus hispidus* [= *Chaetodipus hispidus*] Baird, 1858] 1 male (USNM). **San Saba Co.:** Colorado Bend State Park, ex *P. pectoralis*, 24 males, 22 females (CNC). **Sutton Co.:** ex *Peromyscus eremicus* Baird, 1858, 1 male, 1 female (CNC), 1 male, 1 female (REL), 1 male, 1 female (USNM). **Travis Co.:** ex "rodent nest," 1 female (REL). **Uvalde Co.:** Garner State Park, ex *Peromyscus* sp., 1 male (MWH).

Remarks.—A comparison of specimens from central Texas with those from Nuevo León and San Luis Potosí demonstrates little variation in either sex. Specimens from San Luis Potosí represent the known southern limits of this species. This species and *J. ironsi* are sympatric in the northern range of *J. ironsi*. *Peromyscus pectoralis* appears to be the preferred host of *J. bullisi*. Although a number of unidentified species of *Peromyscus* were listed as hosts, the importance of *P. pectoralis* is evident by the large series taken in San Saba County, Texas. *Jellisonia bullisi* and *J. ironsi* are closely related species, each sharing a similar bifurcate dorsal median lobe of the aedeagus (Fig. 7B, 7D) and a long sigmoid-shaped bursa copulatrix (Fig.

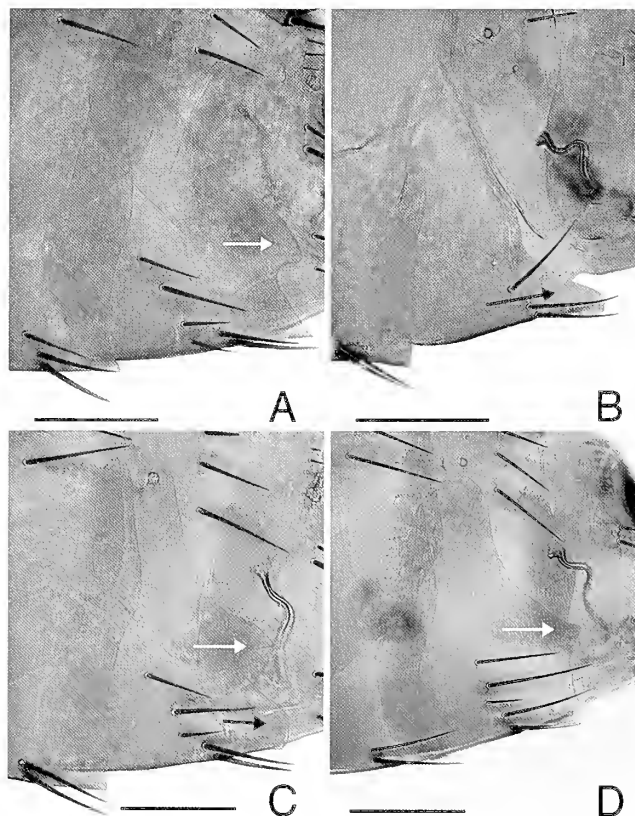


Fig. 20.—Female sternites VI and VII of *Jellisonia* species (white and black arrows = dorsal and ventral lobes of sternum VII, respectively): A, *J. tiptoni*; B, *J. bullisi*; C, *J. grayi*; D, *J. ironsi*. (Scale = 200 μ).

21C, 22H); however, *J. bullisi* has never been recorded on *B. taylori* and *J. ironsi* is recorded only once on *P. pectoralis*.

Jellisonia (*Pleochaetoides*) *grayi* Hubbard, 1958, new
subgeneric combination
(Fig. 4E, 7C, 11B, 14F, 17E, 20C, 22G, 23B)

Jellisonia grayi Hubbard, 1958. Entomological News, 69:163. Ayala-Barajas et al., 1988:67; Ponce-Ulloa and Llorente-Bousquets, 1996:558.

Type Material.—MÉXICO. San Luis Potosí: El Salto, ex *Peromyscus boylii* (Baird 1855), 15 December 1955, C. Hayden (holotype male/allotype female) (BMNH).

Diagnosis.—Male: This is a distinctive species and easily separated by the large lanceolate ventral inverse seta, extreme width of distal arm of sternum IX, and the evenly rounded and protruding ventral lobe of the telomere (Fig. 11B, 14F). Female: The distinction of having a single seta in dorsal notch number seven of the metatibia (counting from proximal) is shared only by *J. bullisi*. The caudal margin of sternum VII has two broadly rounded lobes compared to only a ventral lobe in *J. bullisi* (Fig. 20B–C).

Material Examined.—MÉXICO. Guerrero: Chilpancingo, ex *Peromyscus thomasi* [= *M. thomasi*], 2 females (UNAM). Queretaro: NW

Santa Inés, ex *P. boylii*, 1420 m, 3 females (UNAM). San Luis Potosí: El Salto, ex *P. boylii*, holotype, allotype, 2 male, 1 female paratypes (BMNH), 1 male paratype, ex *Sigmodon hispidus* Say and Ord, 1825, 1 female paratype (USNM); 3 km NE El Salto, 15 km N Naranje, ex *Peromyscus* sp., 1 male, 3 females (BMNH), 13 males, 11 females (CMNH), 2 males, 1 female (CNC), 24 February 1963, R. Traub, 2 males, 2 females (REL), 1 male, 15 females (USNM). Tamaulipas: [Slide labeled "Tamps." interpreted as state of Tamaulipas, Mexico], ex mouse nest, 1 male (CMNH).

Remarks.—The crochet of this species is unique in the finely spiculated, nearly feather-like apex (Fig. 7C), the ventral inverse seta is extremely broad and lanceolate (Fig. 14F), and the telomere bears a distinct denticle on the anterior margin about one-fourth the distance from the apex (Fig. 11B). The disjunct distribution of this species supports the need for additional collecting. Neither the host preference, nor distribution can be inferred with existing data.

Jellisonia (*Pleochaetoides*) *ironsi* (Eads 1947), new
subgeneric combination
(Fig. 1F, 4F, 7D, 11C, 15A, 17F, 20D, 22H, 23A)

Trichopsylla (*Pleochaetis*) *ironsi* Eads, 1947. Annals of the Entomological Society of America, 39:545–548.

Jellisonia ironsi (Eads): Randolph and Eads, 1946:599; Traub, 1950:20–21; Barrera, 1953:217–218; Hubbard, 1958:163; Smit, 1958:205–206; Ayala-Barajas et al., 1988:69; Ponce-Ulloa and Llorente-Bousquets, 1996:558.

Type Material.—UNITED STATES OF AMERICA. TEXAS. Lavaca Co.: Yoakum, ex *Baiomys taylori*, 21 March 1946, R.B. Eads [The holotype and allotype were deposited in the Texas Department of Health, Austin, Texas and can not be located. A specimen in the USNM is labeled "paratype" and has the same data as the holotype. It is hereby designated as the neotype and remains in the USNM.]

Diagnosis.—Male: *Jellisonia ironsi* and *J. bullisi* exclusively share a bifurcate median dorsal lobe (Fig. 7C–D). The latter has nine dorsal notches on the metatibia opposed to *J. ironsi* with eight. Female: This taxon differs from all species in the genus by the pointed shape of the dorsocaudal lobe and very weak subtending concavity of sternum VII (Fig. 20D).

Material Examined.—UNITED STATES OF AMERICA. Bexar Co.: Salado Creek, Fort Sam Houston, ex *Microtus* sp., 1 male (BYU); Misty Park Street, NW San Antonio, ex *B. taylori*, 1 male (MWH); Lackland Air Force Base, San Antonio, ex "*Neotoma* nest," 3 males (MWH); San Antonio, ex *S. hispidus*, 1 male (FSCA). Coryell Co.: ex *B. taylori taylori* [= *B. taylori*], 5 females (USNM), ex *Dipodomys elator* Merriam, 1894, 2 females (USNM), ex *Mus musculus* Linnaeus, 1758, 1 female (USNM), ex *Peromyscus leucopus* Rafinesque, 1818, 2 females (USNM), ex *B. taylori taylori* [= *B. taylori*], 1 male, 2 females (CNC), 2 females (GML), 1 male, 1 female (MWH), ex *B. taylori taylori* [= *B. taylori*], 1 female (BMNH). Dallas Co.: 2.4 km W Desoto, ex *B. taylori*, 15 February 1988, McAllister, 4 females (BMNH). Johnson Co.: 17 km SW Cleburne, ex *B. taylori*, 6 November 1987, 1 male, 1 female (BMNH); 19 km SW Cleburne, 26 September 1987, 1 male, 1 female (BMNH); 25 October 1987, 1 male, 6 November 1987, 3 males, 1 female (REL), ex *Cryptotis parva* (Say 1823), 16 November 1987, 2 females (REL), ex *P. leucopus*, 14 November 1987, McAllister, 1 female (REL); 11 March 1988, 1 male, 1 female (REL), ex *P. maniculatus*, 11 March 1988, 3 males, 4 females (REL), ex *Reithrodontomys montanus* (Baird 1855), 11 March 1988, 5 males, 5 females (REL). Lavaca Co.: Hallettsville, ex *B. taylori*, 1 male, 1 female (CNC), 1 male

paratype; Yoakum, ex *B. taylora*, 2 male, 2 female paratypes (CMNH), 4 male, 4 female paratypes (USNM), 1 male, 1 female paratype (BMNH). **San Patricio Co.:** Welder Wildlife Refuge, Sinton, ex *B. taylora*, 5 males, 4 females (CNC), ex *Reithrodontomys* sp., 1 male, 2 female (CNC). **San Saba Co.:** Colorado Bend State Park, ex *P. pectoralis*, no date, A. Santos, 1 male (REL). **Somervell Co.:** 5 km NNE Nemo, ex *B. taylora*, 1 male (REL). **County Unknown:** Roatun [?], ex *B. taylora*, 1 female (USNM).

COSTA RICA. Cartago: Mt. Irazu, 4.8 km below end of road to crater, 3140 m, ex *Peromyscus* sp., 4 females (CMNH). **Alajuela:** San Jose, Juan Rafael Cabeza, 1220 m, ex *Peromyscus* sp., 3 females, ex "rat," 3 females (CMNH).

GUATEMALA. Jutiapa: 1.6 km SE Jutiapa, ex *Baiomys* sp., 1 female (CMNH).

MÉXICO. Chiapas: Comitán, ex *Baiomys musculus*, 1 female (BMNH); Tinitaria, ex *B. musculus*, 1 female (USNM). **Distrito Federal:** Cerro Zacayuca, ex *B. taylora*, 1 female (BMNH), 1 male, 1 female (CMNH), 2 female (USNM). **Durango:** Peña de Aguila, ex *Peromyscus* sp., 1 male, 1 female (CMNH), ex *Reithrodontomys* sp., 1 male, 2 females (CMNH), ex *Peromyscus* sp., 1 female (USNM); 4.4 km SE Atotonilco, 2036 m, ex *B. taylora*, 26 July 1967, M.K. Petersen, 2 females (REL). **Jalisco:** Zapotlanejo, 1677 m, ex *Mus* sp. or *Baiomys* sp., 4 females (MWH), ex *Baiomys* sp., 17 December 1959, R Traub, 19 December 1959, R. Traub, 1 male, 3 females (REL), ex *Baiomys* sp., 3 females, ex *Mus* sp., 9 females, ex *Peromyscus* sp., 1 female, ex *Sorex* sp., 1 female (USNM). **México:** Tlalcapantla, 2300 m, ex *Baiomys* sp., 1 male, 5 females (UNAM). **Morelos:** Huatla, south of Cuernavaca [Cuernavaca], ex unknown, 1 male, 1 female (MWH); Tepoztlán, ex *Baiomys* sp., 1 male, 2 females (UNAM). **Nayarit:** San Cayatano, 8 km W Tepic, ex *Peromyscus* sp., 3 females (USNM), 1 male, 1 female (CMNH), 1.6 km W Tepic, 793 m, ex *Baiomys* sp., 1 male, 2 females (CNC), ex *Mus* sp., 1 female (CMNH), ex *Cryptotis* sp., 1 male (CMNH). **Oaxaca:** 4.8 km E Oaxaca, Benito Juárez National Park, Cerro San Felipe, 1680 m, ex *B. m. musculus* [= *B. musculus*], 1 male, 1 female (CMNH); 15 km NW Miahuatlán, 1600 m, 1 male, 1 female (UNAM); Monte Albán, 1830 m, ex *B. m. musculus* [= *B. musculus*], 1 female (CMNH), 1 female (USNM). **Puebla:** Matamoros, ex *Baiomys* sp., 1 female (MWH). **San Luis Potosí:** El Salto, 11.2 km N Naranje, ex "mouse nest under stone," 1 male, 3 females (USNM), 1 male (BMNH), ex *B. taylora*, 2 males (CNC); 3.2 km E El Salto, 14.5 km N Naranje, ex *B. taylora*, 1 male, 1 female (CMNH). **State Unknown:** Cerro de la Caldera, 2300 m, ex *B. taylora*, 1 male (UNAM).

Remarks.—*Jellisonia ironsi* is the most widely distributed species in the genus, occurring from Dallas County, Texas, to near the border of Alajuela and Cartago Provinces, Costa Rica. The Costa Rican records are remote from the nearest records in Guatemala. This small series (females only) is indistinguishable from females from Guatemala, Chiapas, Mexico, and Texas, U.S.A. The preferred host for *J. ironsi* is *B. taylora*, occurring throughout its range, although the Costa Rican records are extralimital for *Baiomys*. The three different collections of females from Costa Rica were obtained from a "rat" and from unidentified species of *Peromyscus*. These hosts probably represent *P. mexicanus*, since it is the only species of *Peromyscus* occurring that far south according to Wilson and Reeder (1993). Host species other than *Baiomys* are likely accidental associations. Although *Jellisonia* is typically found in montane habitats, *J. ironsi* is common at very low elevations as well as at higher elevations. This is undoubtedly a reflection of the broad altitudinal distribution patterns of *Baiomys*.

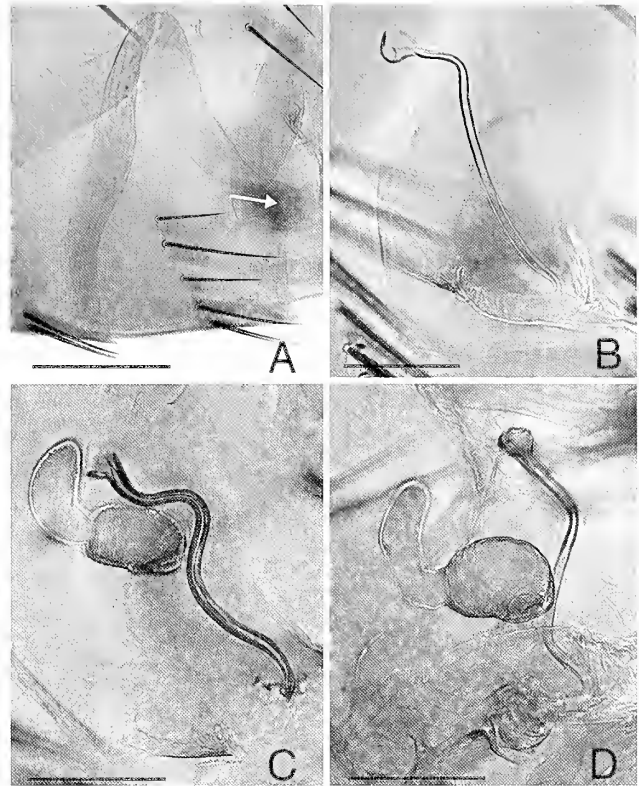


Fig. 21.—Female features of *Jellisonia* and *Kohlsia* species: A, Sternites VI and VII (white arrow = dorsal lobe of sternum VII), *J. wisemani* (Scale = 200μm); B, Bursa copulatrix, *Kohlsia pelaezi*; C, Spermatheca and bursa copulatrix, *J. bullisi*; D, Spermatheca and bursa copulatrix, *J. falcaia* (allotype). (Scale = 100μm).

Jellisonia (*Pleochaetoides*) *mexicana* Ponce-Ulloa,
1989, new subgeneric combination
(Fig. 4G, 8A, 11D, 15B, 24B)

Jellisonia mexicana Ponce-Ulloa. 1988. Folia Entomológica Mexicana, 76:181–185. Ponce-Ulloa and Llorente-Bousquets, 1996:558, 564.

Type Material.—**MÉXICO. Guerrero:** Nueva Delhi, 1400 m, ex *N. mexicana*, 26 March 1984, HP/JJG (holotype male, allotype female) (UNAM).

Diagnosis.—Males: A combination of nine dorsal tibial notches (opposed to eight), a non-bifurcate median dorsal lobe, and a vestigial sternum VIII without setae characterize only *J. mexicana*, *J. wisemani*, and *J. amadoi*. It differs from the latter species in the absence of a "mane" on the mesonotum, metanota, and tergum I. The major difference in *J. wisemani* is the shape of the median dorsal lobe, which is broadly rounded in *J. wisemani* and narrows towards the apex in *J. mexicana* (Fig. 8A–B). Females of *J. ironsi*, *J. wisemani*, and *J. mexicana* are taxa with two setae in dorsal tibial notch number seven (penultimate fascicle) opposed to one seta. Females inseparable from those of *J. wisemani* but the dorsocaudal lobe on sternum VII is rounded in *J. mexicana* and pointed in *J. ironsi* (Fig. 20D).

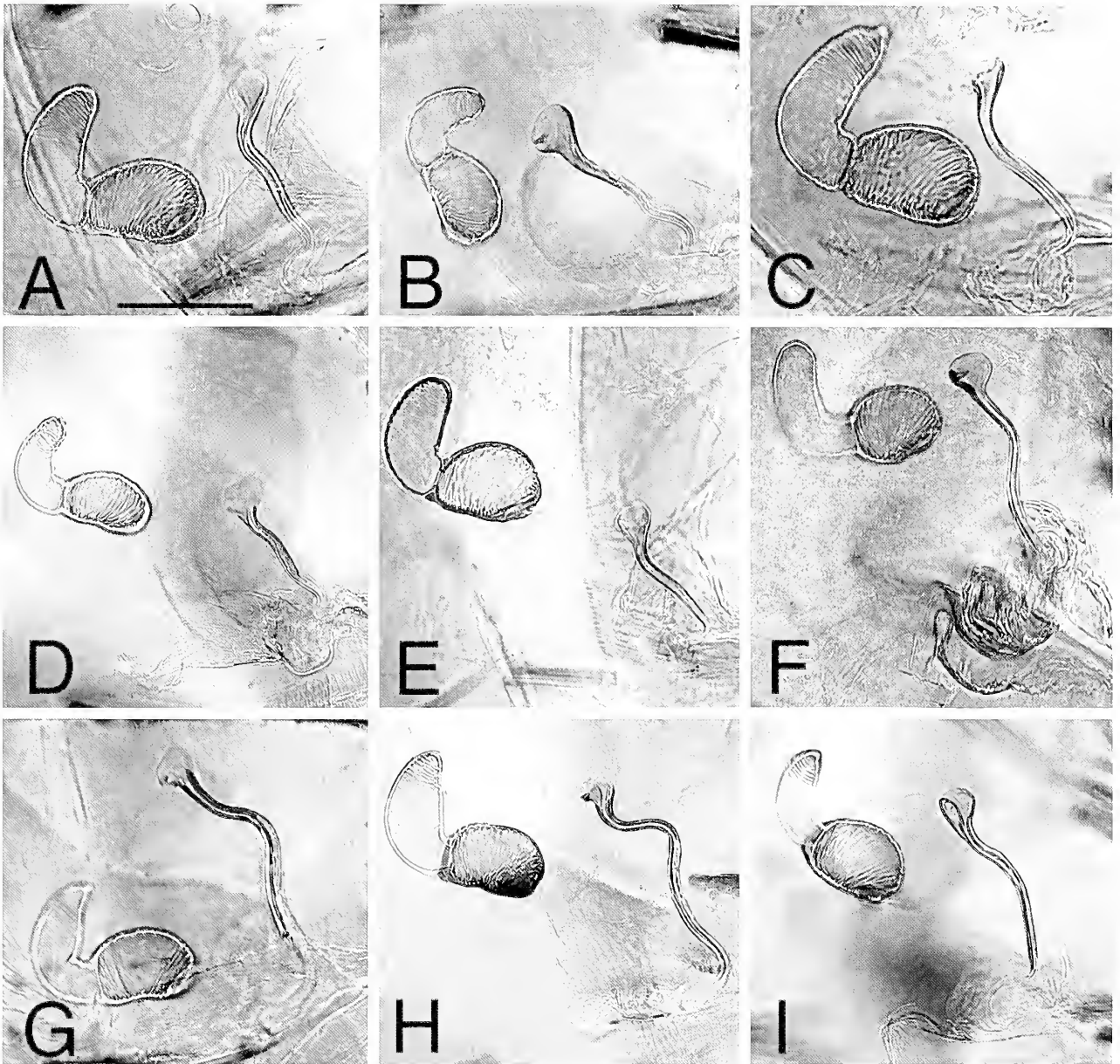


Fig. 22.—Spermathecae and bursae copulatricae of *Jellisonia* species: A, *J. eckerlini* n. sp. (paratype); B, *J. hayesi*; C, *J. jolmsoneae* (paratype); D, *J. maxwelli* n. sp. (paratype); E, *J. painteri* (paratype); F, *J. tiptoni*; G, *J. grayi*; H, *J. ironsi*; I, *J. wisemani*. (Scale = 100μm).

Material Examined.—**MÉXICO. Durango:** Revolucioneros, 2165 m, ex *Peromyscus* sp., 3 males (CMNH); 1.6 km SW Revolucioneros, 1982–2043 m, ex *Peromyscus* sp., 13 males, 5 females (CMNH). **Guerrero:** 8 km E Omiltemi, 1890 m, ex *Peromyscus* sp., 1 male (CMNH). **Jalisco:** 9.7 km W San Marcos, 1646 m, ex *Liomys pictus pictus* [= *Liomys pictus* (Thomas 1893)], 1 male (CMNH). **Nayarit:** 5.5 km E San Blas (Hotel Bucanaro), ex *L. pictus*, 1 male (CMNH), ex *P. eremicus*, 1 female (CMNH). **Sinaloa:** 1 km NE Santa Lucía, 1128 m, ex *Liomys pictus escuinapae* [= *L. pictus*], 1 female (CMNH); ex *P. b. spicilegus* [= *P. spicilegus*], 9 males, 13 females (CMNH), ex *Reithrodontomys fulvescens tenuis* [= *R. fulvescens* J.A. Allen, 1894], 6 males, 1 female (CMNH); 5 km NE Santa Lucía, 1524 m, ex *P. b. spicilegus* [= *P. spicilegus*], 2 males (CMNH); 1.9 km NE Santa Lucía, ex *L. pictus*, 1 male (CMNH); 1.9 km NE Santa Lucía, ex unknown, 3 males, 1 female (CMNH); 1.6

km E Pánuco, ex *N. mexicana*, 1 male (CMNH). **Sonora:** 12.9 km SSE Alamos on Río Cuchujaquí, ex *L. pictus*, 1 male (CMNH).

Remarks.—This is the only species in the genus in which the paired lateral lobes of the aedeagus extend well beyond the apex of the median dorsal lobe. The shape of the lateral lobes is quite variable. These lobes are narrower in some specimens than others. The width of these lobes is determined by the depth of the shallow sinus in the ventroapical margin. The male from the state of Nayarit has a more oblique ventroapical margin than other specimens. Throughout its range, it frequents a number of different host species without obvious preference.

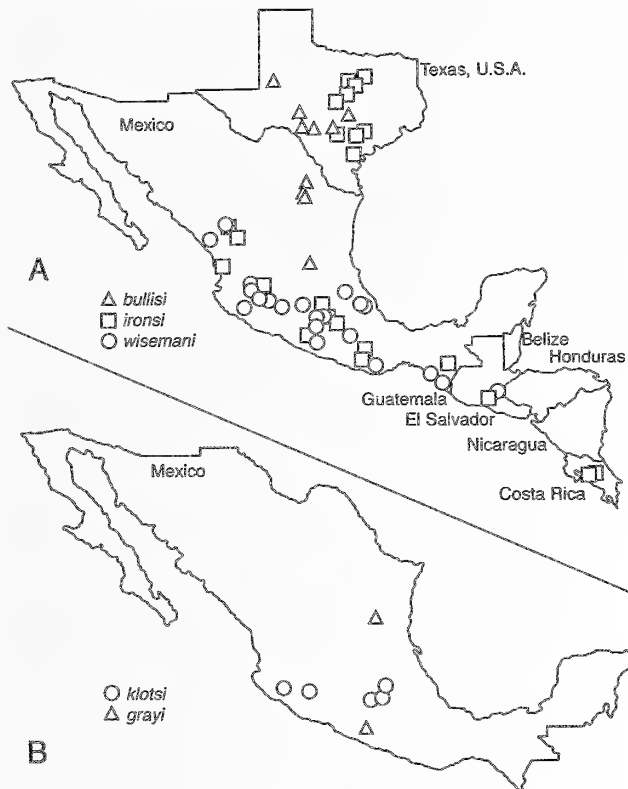


Fig. 23.—Maps illustrating known distribution of *Jellisonia* species: A, *J. bullisi*, *J. ironsi*, and *J. wisemani*; B, *J. klotsi* and *J. grayi*.

Jellisonia (*Pleochaetoides*) *wisemani* Eads, 1951, new subgeneric combination
(Fig. 4H, 8B, 12A, 12B–G, 15C, 21A, 22I, 23A)

Jellisonia wisemani Eads. 1951. *Journal of Parasitology*, 37:147–150. Barrera, 1953:218 [not examined]; Ponce-Ulloa and Llorente-Bousquets, 1996:558.

Jellisonia bonia Traub and Johnson. 1952. *American Museum Novitates*, No. 1558:7–11. Ayala-Barajas et al., 1988:66–67; Ponce-Ulloa and Llorente-Bousquets, 1996:558. New synonymy.

Type Material.—**MÉXICO.** Jalisco: 4.8 km N Guadalajara, ex *Peromyscus melanophrys consobrinus* [= *Peromyscus melanophrys* (Coues 1874)], 19 January 1949, Wiseman (KU), R.H.B., Kansas Museum of Natural History field party (holotype male, allotype female) (USNM No. 60825).

Diagnosis.—Male: A combination of nine dorsal tibial notches (opposed to eight), a non-bifurcate median dorsal lobe, and a vestigial sternum VIII without setae characterize only *J. mexicana*, *J. wisemani*, and *J. amadoi*. It differs from the latter species in the absence of a “mane” on mesonotum, metanotum, and tergum I. The major difference in *J. mexicana* is the shape of the median dorsal lobe that narrows towards the apex in *J. mexicana* and is broadly rounded in *J. wisemani* (Fig. 8A–B). Female: Taxa with two setae in dorsal tibial notch number seven (penultimate fascicle) as opposed to one seta, include *J. ironsi*, *J. wisemani*, and *J. mexicana*. Females of *J. wise-*

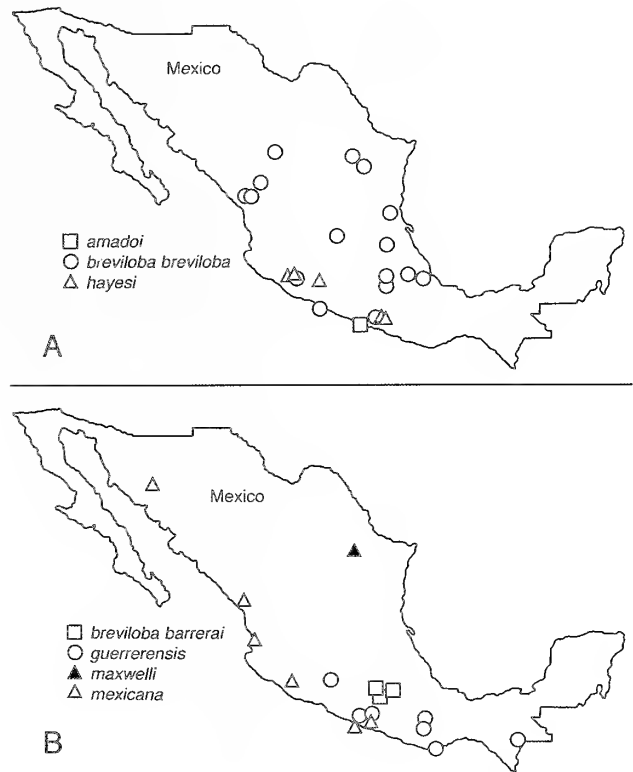


Fig. 24.—Maps illustrating known distribution of *Jellisonia* species: A, *J. amadoi*, *J. breviloba breviloba*, and *J. Hayesi*; B, *J. breviloba barrerae*, *J. guerrensis*, *J. maxwelli*, and *J. mexicana*.

mani are inseparable from those of *J. mexicana* but the dorsocaudal lobe on sternum VII is rounded in *J. wisemani* and pointed in *J. ironsi* (Fig. 20D, 21A).

Material Examined.—**GUATEMALA.** Chiquimula: 2.4 km NW Esquipulas, 945 m, ex *Peromyscus* sp., 2? females (BMNH), 2 males (CMNH); 4 km ENE Esquipulas, 915 m, ex *Peromyscus* sp., 1 female (CMNH), 2 males (BMNH); 4 km ENE and 4.8 km SE Esquipulas, ex *Oryzomys* sp., 1 male (CMNH).

MÉXICO. Chiapas: Volcán Kagchiná, 3.5 km N las Margaritas, 1500 m, ex *Neotoma mexicana chamula* [= *N. mexicana*], 3 males, 5 females (CMNH); Cueva Santa Rosa, 2 km N, 3 km W las Margaritas, 1500 m, ex *N. m. chamula* [= *N. mexicana*], 1 male (CMNH); Cueva Llano Ridondo, 3 km N las Margaritas, 1500 m, ex *N. m. chamula* [= *N. mexicana*], 1 male, 1 female (CMNH); Pan American Highway over Río San Gregorio 32 km from Guatemalan border, *Neotoma ferruginea* [= *N. mexicana*], 2 males (CMNH). Durango: Peña de Aguila, 1921 m, ex *Peromyscus* sp., 3 males (CMNH). Jalisco: Calderon Hacienda, 13 km E Zapotlanejo, 39 km S Guadalajara, 1738 m, ex *Baiomys* sp., 2 males (CMNH), ex *Peromyscus* sp., 1 male, 1 female (CMNH), 1 female (USNM), ex *Rattus* sp., 4 males, 1 female (CMNH); Zapotlanejo, 39 km S Guadalajara, 1677 m, ex *Peromyscus* sp., 18 males, 20 females, ex *Reithrodontomys* sp., 2 males (CMNH), ex *Sorex* sp., 1 male, 2 females (CMNH); 5.6 km WNW Zapotitlán, 1555 m, ex *L. pictus*, 1 male (CMNH); Huascato, ex *Bassariscus* sp., 2 males (UNAM). Guerrero: La Jolla, Cacahuamilpa, ex “nest of *Peromyscus*,” 2 males, 2 females (UNAM), 2 males, 1 female (CMNH); 4.8 km E Omiltemi, 1912 m, ex *Peromyscus* sp., 1 male (CMNH); 8 km E Omiltemi, ex *Peromyscus* sp., 4 males, 6 females (CMNH); 16 km S Taxco (near Telcalpuco), 1400 m, ex *Peromyscus* sp., 1 male, 4 females (CMNH). Michoacán: 18 km W Jiquilpan, 2043 m, ex *P. boylii*, 1 male, 1 female (BMNH), 1 male (CNC); Cerro Guyman, ex *Peromyscus* sp.,

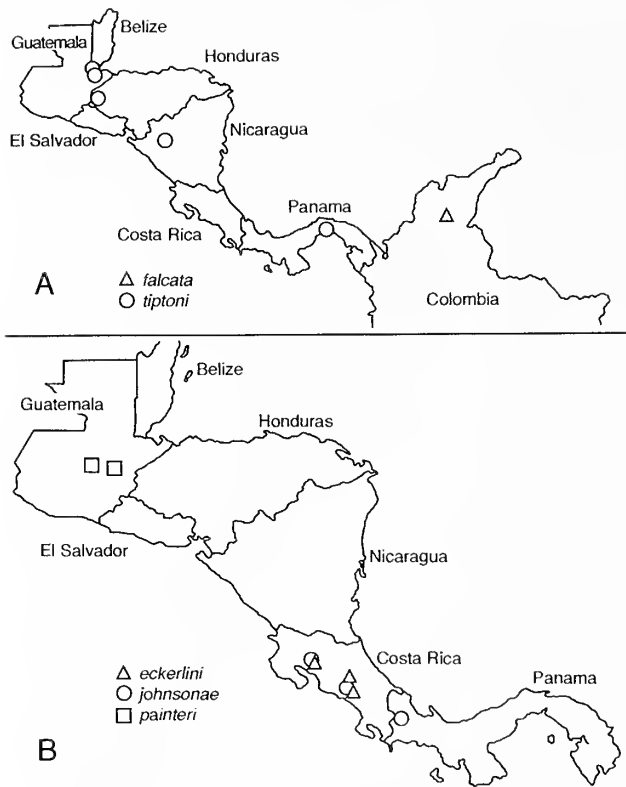


Fig. 25.—Maps illustrating known distribution of *Jellisonia* species: A, *J. falcata* and *J. tiptoni*; B, *J. eckerlini*, *J. johnsonae*, and *J. painteri*.

1 male (CNC), 1 female (CMNH); 11.3 km S Tambisiatio, 823 m, ex unknown, 1 female (CMNH); 4.8 km NE Patzcuaro, ex *Sigmodon* sp., 1 male (CMNH); 4.8 km SW Turundeo, 1900 m, ex *Peromyscus* sp., 1 male (UNAM); 13 km SW Jacona, ex *Reithrodontomys* sp., 1 female (UNAM). **Oaxaca:** Huajuapán de León, 1730 m, ex *Peromyscus* sp., 1 male, 1 female (CMNH); 10 km SE Miahuatlán, ex *P. melanophrys*, 4 males, 6 females (CMNH); Monte Albán, 1829 m, ex *P. maniculatus fulvus* [= *P. maniculatus*], 1 male, 1 female (CMNH), ex *P. truei* [= *P. gratus*], 3 males, 2 females (UNAM). **Morcos:** Tepoztlán, ex *P. lylocetes* = *P. aztecus*, 1 female (UNAM), ex *Peromyscus* sp., 1 male, 1 female; Derrame Chichinautzin, 2110 m, ex *N. torquata* [= *N. mexicana*], 1 male. **Puebla:** Villa Juárez, Xicotepec [Xicotepec Juárez], 1200 m, ex *Peromyscus* sp., 1 male, 1 female (UNAM). **Veracruz:** El Coderio, Jalapa, ex *Peromyscus* sp., 2 females (UNAM); 4.8 km NE Las Minas, 1200 m, ex *P. mexicanus*, 3 males, 2 females (CMNH). Texolo, ex *Peromyscus* sp., 18 October 1950, G.W. Wharton (*J. bonia*, male holotype) (AMNH).

Remarks.—This species was described by Eads (1951) from one male and seven females. Unfortunately, Eads based his diagnosis of the male on the shape of the telomere, which in the holotype is an anomalous condition, or extreme variation. Subsequently, Traub and Johnson (1952) described *J. bonia*. Following the description of both species, large series were collected from a broad geographical area (southern states of Sinaloa and Durango east to Veracruz and south to Guatemala) to include collection sites near the type locality of *J. wisemani*. Examination of these demonstrate the telomere to be highly variable, to include minor differences in the arrangement of the marginal spiniform setae (Fig.

12A–G). These variations could represent different sub-specific populations but character clines are not apparent. Several notes hand penned by Robert Traub among his collection indicated that *J. bonia* was a synonym of *J. wisemani*. Such comments perhaps substantiate why he never described the female of *J. bonia*, as numerous females were identified on the labels of his slides as *J. bonia*. This species is herein placed as a junior synonym of *J. wisemani*.

Other Species Described in *Jellisonia*

Kohlsia ortizi (Vargas 1951)

Jellisonia ortizi Vargas. 1951. Revista del Instituto de Salubridad y Enfermedades Tropicales. 12(1–4):39–43 [not examined].

Kohlsia ortizi (Vargas): Haddow et al., 1983:98.

Type Material.—**MÉXICO. Chiapas:** Comitán, 1620 m, ex *Peromyscus* sp., 4 December 1949 (holotype female) (INDRE).

Material Examined.—**MÉXICO. Chiapas:** 6 mi NW of Teopisca, 1677 m, ex *P. m. guatemalensis* [= *P. guatemalensis*], 30 August 1953, Furman and Price, 1 female (BMNH).

Remarks.—Haddow et al. (1983) evidently recognized the incorrect generic assignment of this species to *Jellisonia*, since it was listed in their work (p. 98) as *Kohlsia ortizi*. Since rationale was not provided as to why they transferred *J. ortizi* to the genus *Kohlsia*, a discussion is provided here. *Jellisonia ortizi* was described from five females; the male is unknown. The holotype and four paratypes were “deposited in the Instituto de Salubridad y Enfermedades Tropicales and the Instituto de Biología, U.N.A.M.” according to Vargas (1951). None of the type series could be located, despite multiple inquiries and efforts to locate them. Unfortunately, the majority of characters used in the original description of *J. ortizi* are generic characters shared by *Kohlsia* and *Jellisonia*. Examination of one female collected near the type locality of *J. ortizi* matches the illustrations of Vargas (1951) and I believe it to be conspecific. Noteworthy characters that are more commensurate with *Kohlsia* than those of *Jellisonia* include: 1) the structure of the sclerotized portion of the bursa copulatrix (long with a right angle bending cephalad just proximal to perula) (see *Kohlsia pelaezi* Barrera, 1956, Fig. 21B); 2) the appearance of the spermatheca (bulga convex dorsally and ventrally and much shorter than hilla); and 3) the less angular ventral margin of the ventral anal lobe.

DISCUSSION

Most of the extant *Jellisonia* material was examined during this revision (1,261 specimens). Specimens of which the author is aware, but was unable to examine, include: a pair of *J. ironsi* in the collection of Professor J.C. Beaucournu (from Traub’s series from Zapotlanejo,

Jalisco, Mexico, 1959), one female *J. ironsi* reported by Smit (1958) from El Salvador, 1953, ex *B. musculus griseus* [= *B. musculus*], the holotype and 10 paratype males of *J. amadoi* (see Remarks), and the holotype male and 11 paratypes (5 males, 6 females) of *J. mexicana* (see Remarks). There are also a number of specimens catalogued Ayala-Barajas et al. (1988) in the holdings of UNAM that were not examined. These appear to belong to the same series as those that were examined and include approximately 85 specimens (37 males, 48 females). Although the genus was described in 1944, the first specimens collected in 1933 (*J. h. breviloba*) were not described until 1950. During the 1950s, seven species were described, one incorrectly placed in *Jellisonia* (*J. ortizi*), two that are synonymized in this revision (*J. bonia* and *J. dybasi*), and two the status of which is altered herein (*J. h. hayesi* and *J. h. breviloba*). With a frenzy of collecting in the 1960s (736 specimens, or 58% of the total known specimens), only one new species was described (*J. johnsonae*). From 1970 to date, relatively few specimens have been collected (203 specimens, or 16% of the total known specimens); however, four new species were described (*J. amadoi*, *J. guerrensis*, *J. mexicana*, and *J. painteri*). Traub (1950) recognized two groups within the genus (*klotsi/hayesi* complex and the *bullisi/ironsi* complex) that might constitute different subgenera. With the availability of additional material, these two complexes are here treated as subgenera (*Jellisonia* and *Pleochaetoides*).

Gaps in our knowledge of the distribution of this genus and yet undiscovered new species probably exist in the mountain regions of El Salvador, Guatemala, Honduras, Nicaragua, and Panama. The flea fauna of El Salvador, Honduras, and Nicaragua are particularly unexplored. Belize and the Yucatán Peninsula (states of Campeche and Yucatán) have no reported records of *Jellisonia*. The ecological parameters of the mountainous topography and cloud forests of these regions necessary to support the genus are lacking and the genus is probably not represented there.

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ON THE SKULL OF *MASSOSPONDYLUS CARINATUS* OWEN, 1854
(DINOSAURIA: SAUROPODOMORPHA) FROM THE ELLIOT AND CLARENS FORMATIONS
(LOWER JURASSIC) OF SOUTH AFRICA

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ABSTRACT

This paper presents a comprehensive description of the cranial structure of the sauropodomorph dinosaur *Massospondylus carinatus*, based on four well-preserved skulls (including one of a juvenile individual) from the Lower Jurassic Elliot and Clarens formations of South Africa. *Massospondylus* can be distinguished from other basal sauropodomorph dinosaurs by the following combination of primitive and derived cranial character-states: The greatest transverse width of the skull exceeds its dorsoventral height by at least 10 percent. Even in adult specimens, the orbit is proportionately large and the antorbital region proportionately short. The maxilla has a tall, nearly vertical dorsal process, and its medial sheet is narrow anteroposteriorly. A long posterior process of the prefrontal extends along the dorsal margin of the orbit, but the frontal still participates significantly in the formation of the orbital margin. There is a distinct ridge on the dorsolateral aspect of the lacrimal and a knob on the lateral surface of the prefrontal. A partial skull from the Lower Jurassic Kayenta Formation of Arizona previously attributed to *Massospondylus* differs from the South African material in several cranial and dental features and is not referable to this taxon.

KEY WORDS: Dinosauria, Saurischia, Sauropodomorpha, Lower Jurassic, Elliot Formation, Clarens Formation, South Africa

INTRODUCTION

Sauropodomorph dinosaurs first appear in the fossil record during the early Late Triassic (Carnian) (Langer et al. 1999; Yates 2003A; Yates and Kitching 2003). Basal taxa of this clade, which are traditionally grouped together as Prosauropoda Huene, 1920, became the principal large herbivores in Late Triassic and Early Jurassic continental ecosystems worldwide (Galton 1984; Wing and Sues 1992). Skeletal remains of these dinosaurs have been known to science since the first half of the nineteenth century. First named 150 years ago (Owen 1854), *Massospondylus carinatus* is now known from scores of well-preserved specimens from the Lower Jurassic Elliot and Clarens formations (commonly informally grouped together with the Molteno Formation as the “Stormberg Group”) in South Africa and Lesotho, and from the correlative Forest Sandstone Formation in Zimbabwe (Cooper 1981). Cooper (1981) presented a detailed description of its postcranial skeleton. Houghton (1924) and Huene (1932) described (under the specific designation *Massospondylus harriesi*) fragments of a skull that had been destroyed by the blow of a pick during excavation. Later authors (Cooper 1981; Attridge et al. 1985; Crompton and Attridge 1986; Galton 1990; Gow et al. 1990) reported on cranial features of *Massospondylus carinatus* and even attempted reconstructions of the skull, but the cranial structure of this dinosaur, with the exception

of the braincase (Gow 1990), has never been documented in detail.

The present account is based on four well-preserved skulls, which formed part of a suite of specimens briefly reviewed by Gow et al. (1990) and are housed in the collection of the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand in Johannesburg. They are of particular interest because they represent different growth stages. We did not have access to cranial material referable to *Massospondylus carinatus* housed in the collections of the South African Museum in Cape Town. Gow et al. (1990) deemed it unnecessary to provide a detailed account of the skull of *Massospondylus* in view of its overall similarity to that of *Plateosaurus* from the Upper Triassic (Norian) of France, Germany, and Switzerland. As Huene (1932) noted, there exist a number of cranial differences between these taxa, and, in view of their different phylogenetic relationships (Yates 2003B), a comprehensive description of the skull of *Massospondylus* is clearly warranted. Throughout the following description, comparisons are made with the skull of *Plateosaurus*, which is currently the best known basal sauropodomorph dinosaur. These comparisons draw on the detailed, profusely illustrated descriptions by Huene (1926) and Galton (1984, 1985) and on our examination of

an excellently preserved, disarticulated skull referable to *P. longiceps* (AMNH 6810).

In this paper, we employ the standard directional terminology of comparative anatomy rather than that of veterinary anatomy now used by some students of dinosaurian anatomy. Furthermore, for teeth, "mesial" denotes toward the mandibular symphysis and "distal" toward the jaw joint.

INSTITUTIONAL ABBREVIATIONS

AMNH—American Museum of Natural History, New York

BP—Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Sauropodomorpha Huene, 1932

Massospondylidae Huene, 1914 *sensu* Yates, 2003B

Massospondylus carinatus Owen, 1854

Holotype.—The holotype of *Massospondylus carinatus* formed part of a suite of postcranial skeletal remains, representing at least two individuals, discovered by Dr. R.J.N. Orpen and Mr. J.M. Orpen on the farm Beauchef (frequently incorrectly given as "Beaucherf") Abbey in the Harrismith District of South Africa (28° 31'S 29° 10'E; straddling the boundary between 1:50000 map sheets 2829CA Harrismith and 2829CA Oliviershoek). This material was subsequently sent to the famous Museum of the Royal College of Surgeons in London (Seeley 1895; Cooper 1981). Owen (1854:97–100) briefly described (without illustration) this material, which comprised some 55 catalogued bones and fragments of bone, and somewhat arbitrarily assigned these remains to three separate taxa, *Massospondylus carinatus*, *Pachyspondylus orpeni*, and *Leptospondylus capensis*. He considered the three forms to have lacertilian affinities. Seeley (1895) argued that Owen's specimens represented but a single taxon, *Massospondylus carinatus*, which he explicitly compared to *Zanclodon*, which was the common generic designation for most Late Triassic sauropodomorphs from Germany at that time. Huene (1906) concurred with Seeley's assessment and described a number of bones in more detail. Owen's material of *Massospondylus carinatus* was derived from strata of the upper Elliot Formation (Kitching and Raath

1984: table 1). It was destroyed during a German air raid on London during World War II, but plaster casts of at least some of Owen's specimens had previously been distributed to and are still preserved in other museums (Huene 1906; Cooper 1981). In view of the fragmentary nature of Owen's (now lost) original material, we consider it advisable to designate a neotype for *Massospondylus carinatus*, but this step must await a comprehensive revision of all basal sauropodomorph dinosaurs from the "Stormberg Group" of South Africa. Specimen BP/1/4934, comprising a well-preserved skull and much of the postcranial skeleton of a large individual, would be an excellent candidate for a neotype.

Distribution.—The known stratigraphic range of *Massospondylus carinatus* extends from the middle Elliot to the lower Clarens formations (*Massospondylus* Range Zone) of the "Stormberg Group" (Kitching and Raath 1984). These units are considered Early Jurassic in age (Olsen and Galton 1984).

Attridge et al. (1985) referred a badly crushed but otherwise well-preserved partial cranium and mandible (MCZ 8893) from the Lower Jurassic Kayenta Formation of Arizona to *Massospondylus*. Our examination of this specimen, however, revealed several differences in cranial and dental features from the South African material that cast doubt on the validity of the original generic assignment. A reassessment of MCZ 8893 will be presented elsewhere.

The alleged occurrence of *Massospondylus* in the Lower Jurassic McCoy Brook Formation of Nova Scotia, Canada (Russell 1989), cannot be confirmed. Although the sauropodomorph material from that unit has yet to be studied in detail there is nothing to suggest its referral to *Massospondylus* (H.-D.S., pers. obs.).

Referred Specimens in this Study.—BP/1/4376 represents the smallest skull used in this study (Gow et al. 1990: fig. 3; Figs. 1 and 2). Cooper (1981:fig. 3) first presented a slightly diagrammatic drawing of this skull. It is associated with a considerable quantity of postcranial bones (Gow et al. 1990). Only the right side of the skull, including most of the right mandibular ramus and first ceratobranchial, is completely preserved. Many cranial bones on the left side are incomplete, displaced, or missing. The skull has been strongly compressed laterally during fossilization. Based on its small size (skull length: 94 mm) as well as its proportionately very large orbits and short snout, we consider BP/1/4376 a juvenile specimen of *Massospondylus carinatus*.

As a result of obliquely dorsoventral crushing during fossilization, the skull of BP/1/4779 (Gow et al. 1990:fig. 4; Figs. 3 and 4) appears wider transversely than the other specimens. It has also been compressed anteroposteriorly, especially in the antorbital region. Otherwise, the skull is complete. Its occipital surface

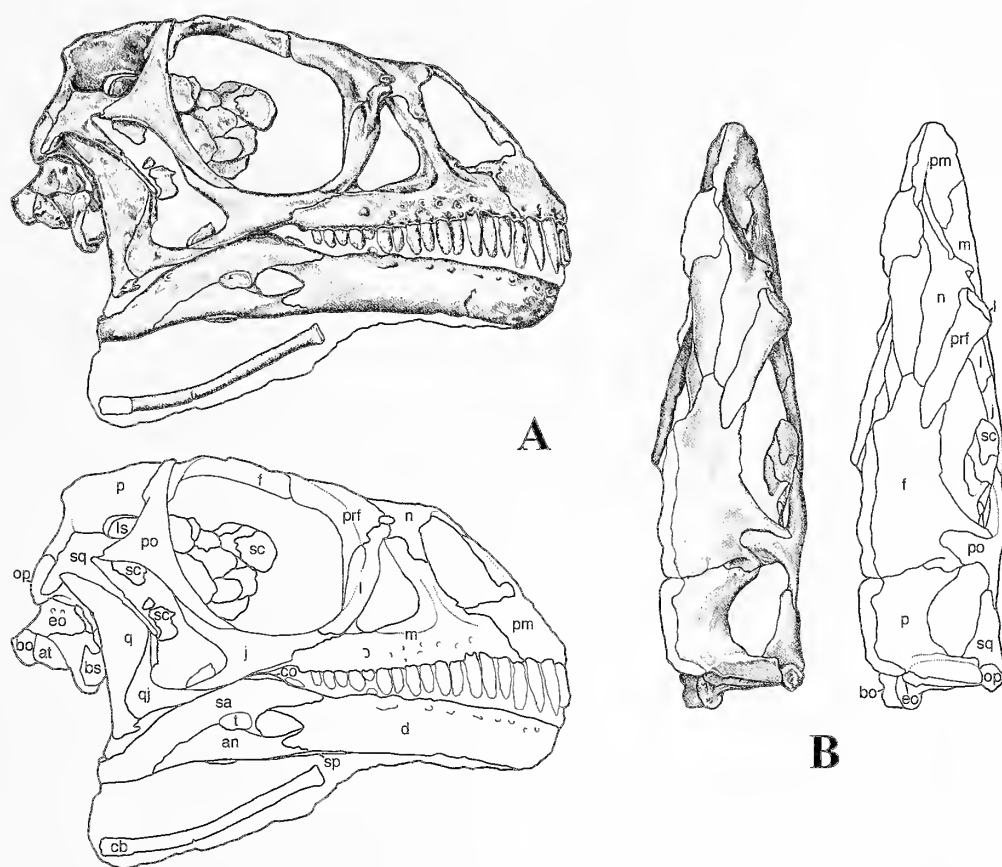


Fig. 1.—Skull of a juvenile specimen of *Massospondylus carinatus* (BP/1/4376) in (A) right lateral and (B) dorsal views, with explanatory diagrams. Scale bar = 5 cm. Abbreviations used in Figures 1–7: an, angular; ar, articular; at, atlantal intercentrum; atn, atlantal neural arch; ax, axis centrum; bo, basioccipital; bs, basisphenoid; c.p, cultriform process of parasphenoid; cb, ceratobranchial I; co, coronoid; d, dentary; ec, ectopterygoid; eo, exoccipital; ep, epipterygoid; f, frontal; fm, metotic foramen; fo, fenestra ovalis; lc, foramen for passage of A. carotis interna; j, jugal; l, laerimal; ls, laterosphenoid; m, maxilla; n, nasal; o.c, occipital condyle; op, opisthotic; os, orbitosphenoid; p, parietal; pa, proatlas; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sc, scleral ossicle; so, supraoccipital; sp, splenial; sq, squamosal; st, stapes; t, tooth; v, vomer. Roman numerals denote exits for cranial nerves.

is partially concealed by the still attached atlas-axis complex.

The skull of BP/1/4934 (Gow et al. 1990:fig. 1; Figs. 5 and 6) is the largest in the sample used in this study (reconstructed skull length: 210 mm) and is associated with much of a skeleton, which lacks only the tail and hind-limbs. In addition to considerable lateral compression, the skull was distorted along the sagittal plane during fossilization. Otherwise, it is well preserved and includes the complete right side of the cranium as well as the braincase. Much of the left side of the snout and skull roof was destroyed, exposing the left wall of the braincase and much of the palate in lateral view. The incomplete left side of the snout was displaced forward relative to the complete right side, and the two mandibular rami became separated at the symphysis.

BP/1/5241 (Gow et al. 1990:fig 2—listed incorrectly as “5247” in the figure legend; Fig. 7), the second largest individual used in this study, comprises a well-

preserved skull (skull length: 175 mm) associated with much of an articulated postcranial skeleton. The skull was strongly crushed laterally during fossilization. Only the more posterior portion of the palate could be exposed during preparation. The occipital region of the skull is, for the most part, concealed by the articulated cervical vertebrae. The mandible is not preserved.

Preservation of the skulls, especially those of BP/1/4934 and BP/1/5241, is generally good. In addition to the preservational deficiencies enumerated above, however, there is considerable small-scale fracturing and displacement of bone due to crushing of individual cranial elements.

Horizon and Locality Data for Referred Specimens.—Gow et al. (1990) provided the following provenance information for the specimens used in this study: BP/1/4376—middle Elliot Formation, Blikana Mountain, Herschel District, latitude 30° 36'S and longitude 27°

37°E (1:50000 map sheet 3027AD Blikana); BP/1/4934—upper Elliot Formation, farm Bormansdrift, latitude 28° 57'S and longitude 27° 26'E (1:50000 map sheet 2827CD Mekoatlengsnek); BP/1/4779—Clarens Formation, farm Tevrede, latitude 28° 32'S and longitude 28° 30'E (1:50000 map sheet 2828CB Clarens); BP/1/5241—Clarens Formation, farm Upper Drumbo, latitude 30° 50'S and longitude 27° 45'E (1:50000 map sheet 3027DC Barkly East).

Diagnosis Based on Cranial Features.—Characterized by the following combination of primitive and derived cranial character-states: Greatest transverse width of skull exceeding dorsoventral height of skull by at least 10 percent. Orbit proportionately large and antorbital region proportionately short even in presumably adult specimens. Dorsal process of maxilla tall and nearly vertical; medial sheet of maxilla narrow anteroposteriorly. Prefrontal with long posterior process along dorsal margin of orbit, but frontal still contributing significantly to formation of orbital margin. Lacrimal with lateral sheet overhanging posterodorsal corner of antorbital fenestra. Distinct ridge on dorsolateral aspect of lacrimal, continuous with lateral knob on prefrontal.

As the structure of the skull in most other named taxa of basal sauropodomorph dinosaurs (Yates 2003B) is still poorly known, it is not clear at the present time at what taxonomic level most of the aforementioned features are diagnostic. For the same reason, it is not possible at present to identify unambiguous cranial autapomorphies for *Massospondylus carinatus*.

DESCRIPTION

The following description is based on examination of all four skulls. The external surfaces of the cranial bones can be readily documented in detail, but most of the interior of three of the skulls could not be examined because it is still filled with matrix. Therefore, the description of the elements comprising the braincase is based primarily on BP/1/4376, which shows the medial surface of the right wall of the braincase and the basicranial region (Figs. 1 and 2), and BP/1/4934 (Figs. 5 and 6), which exposes much of the left lateral wall and occipital surface of the braincase. Additional information on the structure of the braincase is available in Gow's (1990) account, which was based on disarticulated material. Observations of palatal features are based on BP/1/4779 (Fig. 3) and BP/1/4934 (Fig. 5). Individual and ontogenetic variation in structural details is noted where appropriate. Few reliable measurements can be made on the skulls due to often extensive deformation and crushing of these specimens during fossilization (Gow et al. 1990).

Skull

The greatest transverse width of the skull is at the level of the sutural contact between the frontals and parietals. The large external naris is bounded by the premaxilla, maxilla,

and nasal. Its greatest diameter is more than half the maximum diameter of the orbit. The triangular antorbital fossa is bordered by the dorsal process of the maxilla anteriorly, the nasal dorsally, the lacrimal posterodorsally and posteriorly, and the maxilla and jugal ventrally. The large orbit is bounded by the prefrontal, frontal, and postorbital dorsally, the lacrimal and prefrontal anteriorly, the postorbital and jugal posteriorly, and the jugal ventrally. The supratemporal fenestra faces mainly dorsally. It is bounded by the frontal and postorbital anteriorly, the postorbital and squamosal laterally, the parietal medially, and the parietal and squamosal posteriorly. The infratemporal fenestra is shaped like an inverted T, and its long axis extends somewhat anteroventrally. The anteroventral corner of this opening slightly underlies the orbit. The internal narial opening is bordered by the maxilla laterally, the palatine and vomer medially, and the palatine posteriorly. The suborbital fenestra is bounded by the palatine anteromedially, the jugal laterally, and the ectopterygoid posteriorly. The foramen magnum is bordered by the supraoccipital dorsally, the exoccipitals ventrolaterally, and the basioccipital ventrally.

Premaxilla.—The premaxilla forms the transversely narrow, (in ventral view) triangular anterior end of the snout as well as the anteroventral margin of the external naris. Its slender posterolateral process overlaps the subnarial process of the maxilla at the posteroventral corner of the external naris. As a result, the dorsal margin of the body of the premaxilla is longer than its alveolar margin. The suture between the maxilla and premaxilla has the shape of an inverted L and intersects the alveolar margin just behind the fourth premaxillary tooth. A large, elliptical subnarial foramen is situated on the descending segment of this suture well above the tooth row. The transversely flattened dorsal (internarial) processes of the premaxillae taper as they curve posterodorsally and are overlapped by the anterior ends of the nasals posterolaterally. A row of small foramina extends above the alveolar margin, and additional openings are scattered on the anterolateral surface of the rather deep body of the premaxilla. These foramina presumably served as exits for terminal branches of subnarial branches of A. maxillaris and N. ethmoidalis medialis (Oelrich 1956). The narrow palatal surface of the premaxilla is not fully exposed in any of the available specimens. We concur with Yates (2003B) that the premaxilla exhibits no features that would indicate the presence of a rhamphotheca in life. Unlike in the dentary, the alveolus for the first tooth is situated close to the anterior end of the premaxilla, leaving no room for a rhamphotheca.

Maxilla.—The maxilla is triradiate, with a distinct anterior (subnarial) ramus, a long, nearly straight posterior ramus, and a tall, slightly recurved dorsal process, which separates the antorbital fossa from the external naris and is set back from the anterior end of the maxilla. The subnarial ramus of the maxilla forms a shallow fossa at the pos-

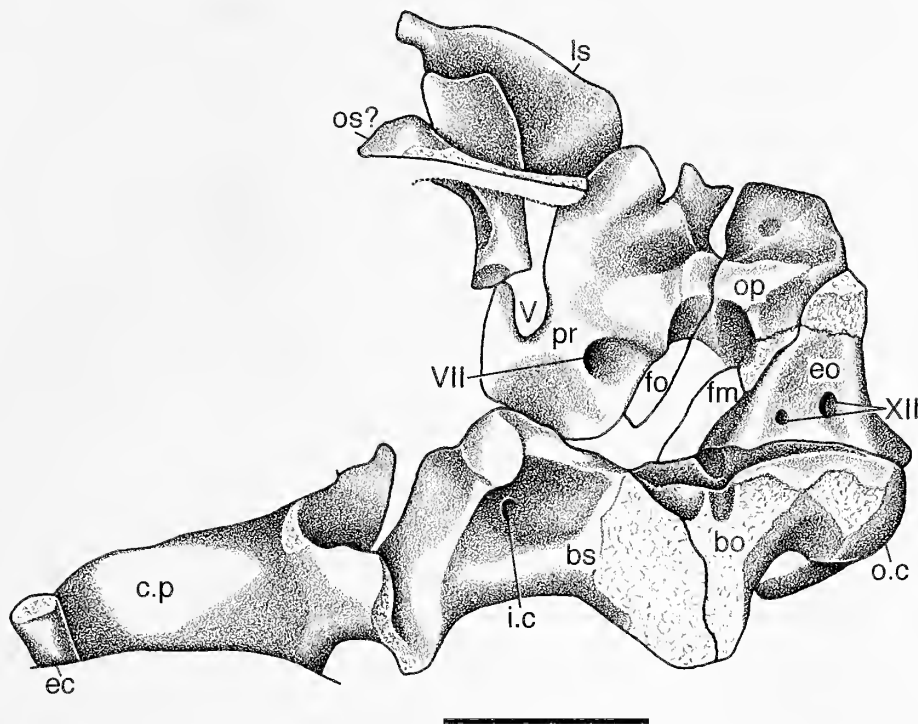


Fig. 2.—Left lateral view of the basicranial region and medial view of the right wall of the braincase of a juvenile specimen of *Massospondylus carinatus* (BP/1/4376). Scale bar = 1 cm.

teroverventral corner of the external naris and at the anteroventral corner of the antorbital fossa. The medial sheet of the maxilla forms the medial wall of the fossa anterior to the antorbital fenestra (internal antorbital fenestra sensu Witmer 1997). The sheet is narrow and distinctly embayed from behind, unlike the broad medial sheet with an almost straight posterior margin present in *Plateosaurus*. The posterior margin of the medial sheet extends more or less parallel to the anterior margin of the antorbital fossa. The nasal overlaps the dorsal process of the maxilla anterolaterally, but the maxilla contacts the lacrimal above the antorbital fenestra. The jugal overlaps the maxilla posterodorsally; the suture between these two bones extends obliquely from the posteroventral corner of the antorbital fenestra back to the level of the posterior part of the orbit. The posterior ramus of the maxilla is low dorsoventrally and, in lateral view, tapers to a point below the posterior half of the orbit. A row of six or seven supralabial foramina extends dorsal and parallel to the alveolar margin of the maxilla. These openings probably served as exits for cutaneous branches of A. maxillaris and N. alveolaris superior (Oelrich 1956). The posterior-most supralabial foramen is the largest and opens posteriorly. The right maxilla of BP/1/4934 has three minute foramina behind this large posterior foramen. In addition to the row of supralabial foramina, one or two additional openings are situated just anterior to the base of the dor-

sal (ascending) process of the maxilla. The medial contact of the maxilla with the vomer is short (BP/1/4779).

Nasal.—Dorsally, the nasals are gently arched above the external nares. The nasal is long, equivalent to about half the total length of the largest skulls. Anteriorly, the nasals are separated by the dorsal processes of the premaxillae, and, more posteriorly, by the intervening frontals. Each nasal is convex transversely, resulting in a longitudinal depression along their median sutural contact. Laterally, the nasal contributes to the lateral edge of the antorbital fossa dorsally and overhangs the dorsal apex of the fossa, forming a deep recess similar to that in *Plateosaurus* (Witmer 1997). The nasal does not have a posterolateral process, unlike in *Plateosaurus* (Yates 2003A:fig. 10B, cl.p). It forms the posterodorsal margin of the external naris and overhangs this opening dorsally. The triangular ventral process of the nasal does not contact the posterior process of the premaxilla, and the maxilla forms the posteroventral margin of the external naris. The right nasal of BP/1/4934 bears two small openings, possibly for passage of cutaneous branches of N. ethmoidalis lateralis, on its dorsolateral aspect; these features are absent on the other skulls used in this study. The anterior foramen opens into an anteriorly extending groove whereas the posterior one has a posteriorly extending groove.

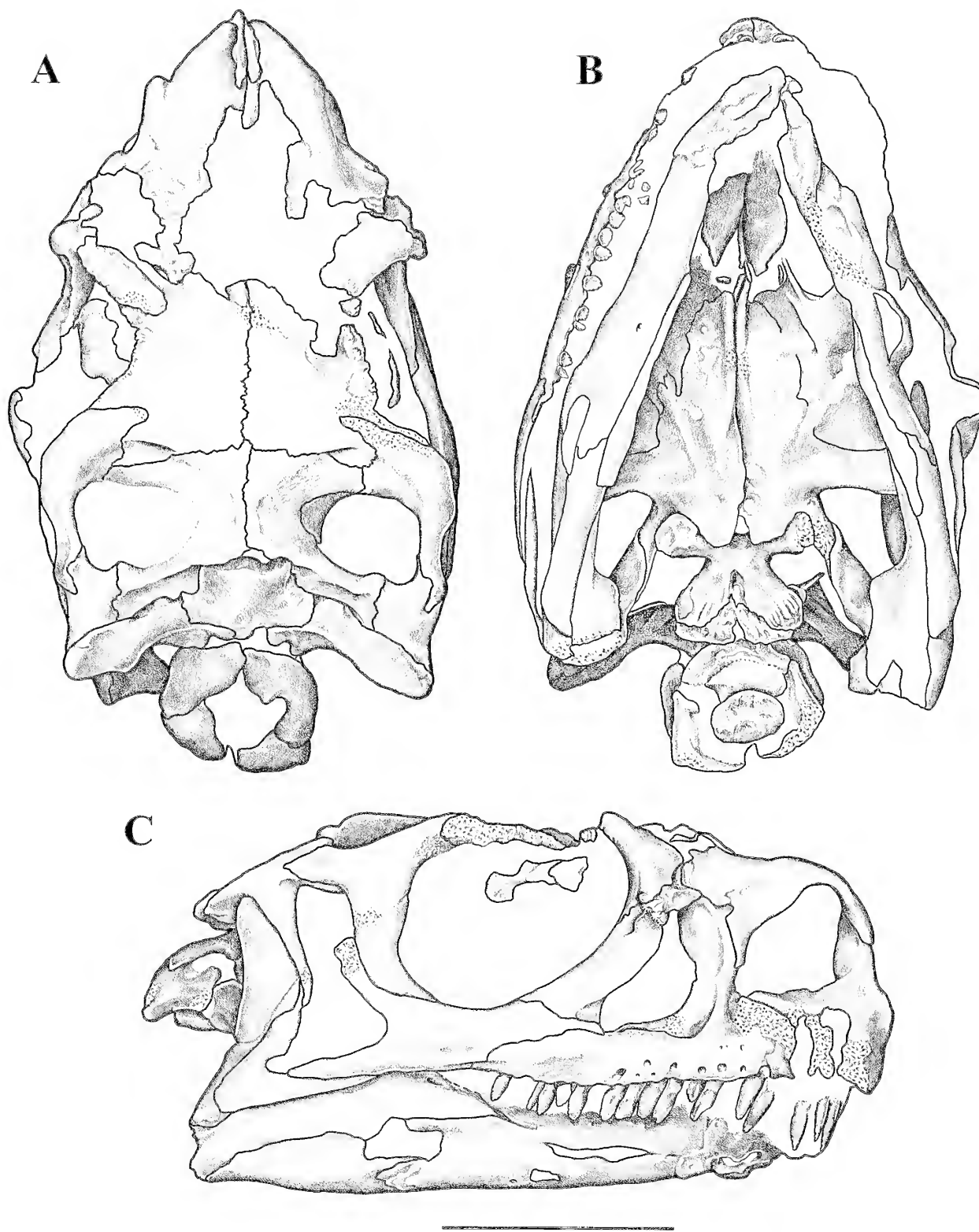
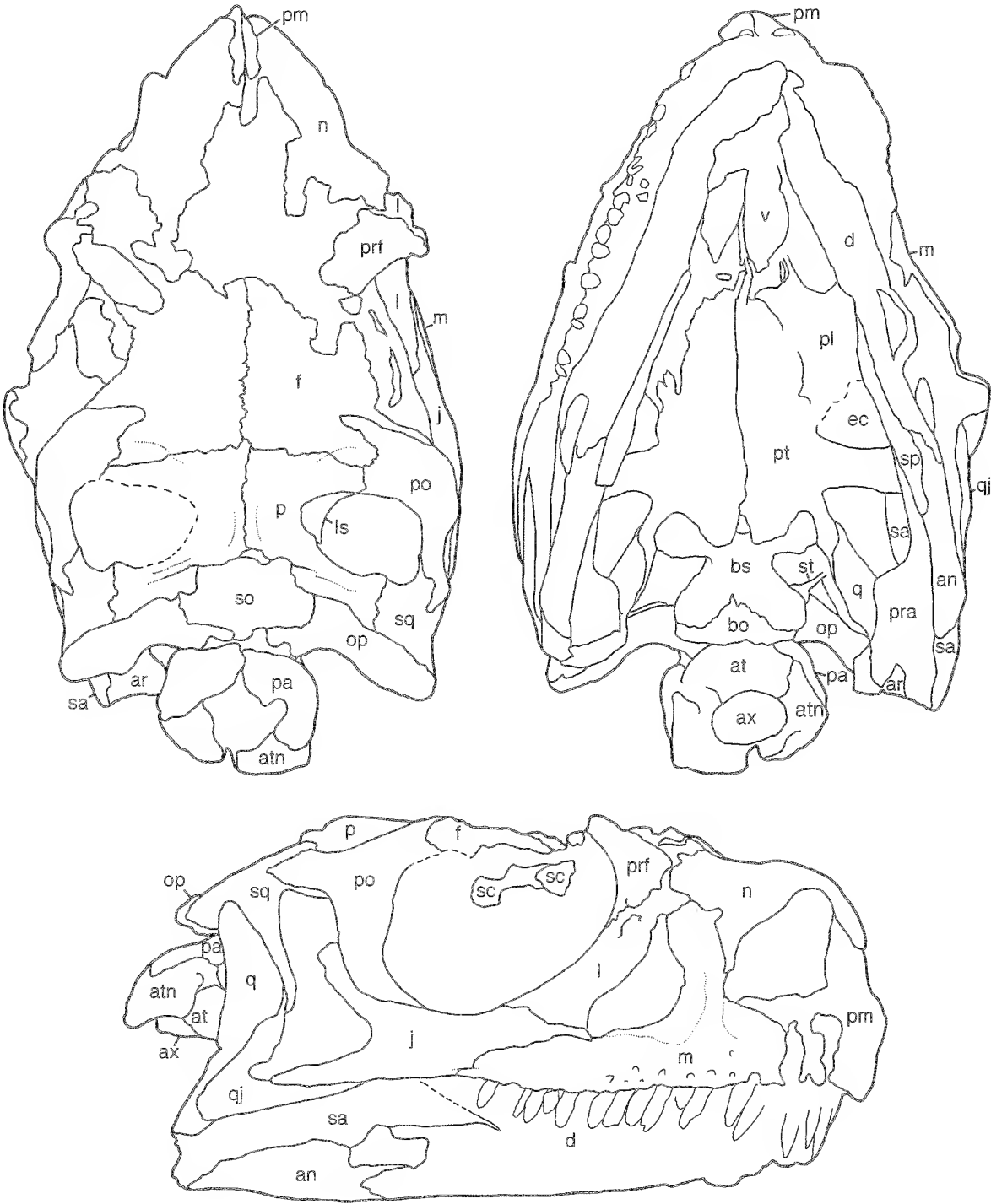


Fig. 3.—Skull of *Massospondylus carinatus* (BP/1/4779) in (A) dorsal, (B) ventral, and (C) right lateral views, with explanatory diagrams. Scale bar = 5 cm.



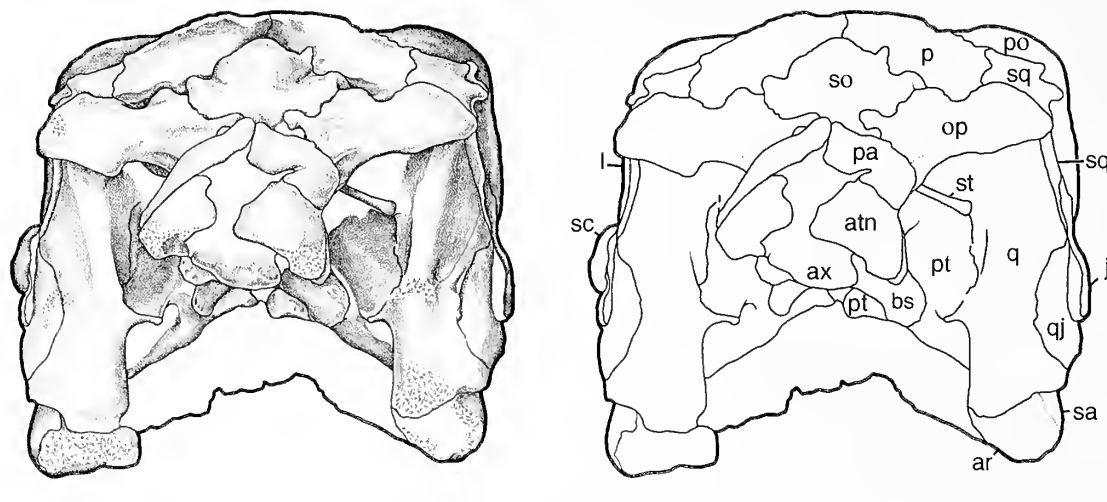


Fig. 4.—Skull of *Massospondylus carinatus* (BP/1/4779) in occipital view, with explanatory diagram. Scale bar = 5 cm.

Prefrontal.—The large prefrontal forms the anterodorsal margin of the orbit. Its dorsal exposure on the skull roof is much more extensive than that of the lacrimal. The prefrontal has a long posterior process, which overlaps the frontal; however, the frontal still makes up about half of the dorsal margin of the orbit. The section of the orbital rim formed by the prefrontal is thick and somewhat rugose. The sutural contact of the prefrontal with the nasal is long and straight, and wraps around the dorsal portion of the lacrimal. A slender, tapering ventral process of the prefrontal extends just medial to, but does not participate in the margin of, the posterior opening of the canal for the nasolacrimal duct and overlaps the postero-medial aspect of the ventral ramus of the lacrimal.

Lacrimal.—In lateral view, the lacrimal is shaped like an inverted L, with a short anterior and a long ventral ramus. It separates the orbit from the antorbital fossa, and is inclined (and, in BP/1/4376 and BP/1/4779, bowed) forward. Dorsally, the lacrimal is narrowly exposed on the skull roof anterior to the prefrontal and lateral to the nasal. Its ventral process is expanded at the distal contact with the jugal. The posteroventral end of the antorbital fossa extends onto the lateral surface of the ventral end of the ventral process of the lacrimal, forming a shallow, triangular ventrolateral depression. This depression extends dorsomedially half way up the ventral ramus in BP/1/5241, but it is small in the juvenile specimen BP/1/4376. The anterior ramus of the lacrimal forms a subtriangular lateral lamina that overhangs the posterodorsal portion of the antorbital fossa. The dorso-lateral surface of the lacrimal bears a ridge, which is most pronounced in BP/1/4934. This ridge is associated with a knob on the lateral aspect of the prefrontal on all four specimens. The posterior opening of the canal for the nasolacrimal duct is situated on the posteromedial aspect of the ventral ramus of the lacrimal below the

junction of that process with the anterior ramus of the lacrimal.

Frontal.—The frontal is longer than wide. It reaches its greatest width posteriorly. The frontal is concave transversely in the interorbital region, which is constricted at mid-length. Its orbital margin is slightly raised and rugose. The median sutural contact between the frontals forms a dorsal ridge. Anteriorly, the frontals are slightly overlapped by the nasals. The anteromedial process of the postorbital fits into an anteromedially extending slot on the dorsal aspect of the posterolateral process of the frontal. Thus the frontal excludes the postorbital from the dorsal margin of the orbit. Posteriorly, the suture between the frontal and postorbital is distinctly interdigitated medially. The supratemporal fossa extends anteriorly onto the frontal, resulting in a crescentic depression on the posterodorsal aspect of that bone.

Parietal.—The paired parietals form the roof of the skull between the supratemporal fenestrae. There is no trace of a pineal foramen. The ridges demarcating the medial margins of the supratemporal fossae are not as pronounced more anteriorly as they are on the wing-like posterolateral processes of the parietals more posteriorly. They enclose between them a narrow, horizontal dorsal surface. Lateral to the median ridge of the supratemporal fossa, the parietal is deflected ventrally. In dorsal view, the posterolateral and anterolateral processes of the parietal separated by a median constriction. The posterolateral process is deflected ventrolaterally and contacts the medial process of the squamosal slightly below the level of the dorsal surface of the skull roof.

Postorbital.—The triradiate postorbital separates the orbit, infratemporal fenestra, and supratemporal fenestra

from each other. The robust anterior and especially the ventral process of this element are longer than its slender posterior process. The anterior process of the postorbital appears to be slightly forked at its medial contact with the frontal, and the supratemporal fossa extends onto its posterodorsal surface. The slender ventral process gently curves anteroventrally and overlaps the dorsal process of the jugal anterolaterally. The tapered posterior process fits into a slot on the lateral surface of the squamosal. The orbital margin of the postorbital is thick and slightly rugose.

Jugal.—The mediolaterally flattened jugal is shaped like a Y lying on its side. Its anterior (infraorbital) process contributes to the posteroventral margin of the antorbital fenestra except in BP/1/4376 where it only reaches the posteroventral corner of the antorbital fossa. The jugal forms a long sutural contact with the maxilla ventrally and overlaps the ventral end of the lacrimal dorsolaterally. Its gently curved dorsal process is placed far back and broad at its junction with the remainder of the bone. It contacts the ventral process of the postorbital.

Squamosal.—The squamosal forms the posterolateral corner of the skull roof. It contacts the posterior process of the postorbital anteriorly, the quadrate and quadratojugal posteroventrally, and the parietal and paroccipital process of the opisthotic medially. Laterally, the anterior process of the squamosal is overlapped by the posterior process of the postorbital. Its short medial process meets the posterolateral wing of the parietal. The ventral process of the squamosal is long and slender. Its dorsal portion bears a triangular recessed area along the posterodorsal corner of the infratemporal fenestra; this area, possibly for the origin of *M. adductor mandibularis externus superficialis* (Ostrom 1961), is most pronounced in BP/1/5241. The tapered ventral end of the ventral process contacts the dorsal end of the quadratojugal along the posterior margin of the infratemporal fenestra. Posteriorly, the squamosal abuts the anterolateral surface of the paroccipital process and caps the dorsal head of the quadrate.

Quadratojugal.—The quadratojugal is roughly V-shaped and thin. It overlaps the quadrate medially and forms the posteroventral corner of the infratemporal fenestra. Its slender anterior (infratemporal) process forms a long sutural contact with the posterior process of the jugal.

Quadrate.—The tall quadrate is gently sigmoidal in lateral view and divided into two parts that extend at nearly right angles to each other. A large, anteromedially directed flange overlaps the pterygoid; the base of this flange is not as deep dorsoventrally as in *Thecodontosaurus* (in which it equals more than 70 percent of the total height of the quadrate; Yates 2003B). A thickened ridge extends

along the posteromedial margin of the bone where the pterygoid flange joins the anterolateral portion of the quadrate that supports the distal articular end of the bone. It terminates dorsally in the small head of the quadrate, which fits into a ventral socket on the squamosal (exposed on the left side in BP/1/4934). A narrow quadrate foramen for the passage of *V. mandibularis* (Oelrich 1956) is incised as a notch into the lateral margin of the quadrate medially and is bounded by the quadratojugal laterally. The posterior surface of the quadrate bears a depression with a central pit or foramen. The distal articular surface of the quadrate is more or less triangular in outline, with the apex of the triangle formed by the lateral corner of the facet and the long axis of the surface extending transversely. It is divided by an antero-medially extending groove into a lateral and a larger medial condyle.

Vomer.—The paired vomer is broad and relatively slightly shorter than in *Plateosaurus* (AMNH 6810). Its ventral surface is gently convex transversely, which sets it off from the transversely concave ventral surface of the palatine more posteriorly. The anterior extent of the element and its contact with the premaxilla could not be exposed during preparation, but, posteriorly, the vomers are wedged between slender, dorsoventrally expanded processes of the pterygoid and palatine.

Palatine.—The palatine forms the central portion of the palate anterolateral to the pterygoid. It makes up the posteromedial margin of the internal naris as well as the anteromedial margin of the suborbital fenestra. In BP/1/4779, a distinct ventral ridge extends along the posteromedial margin of the internal naris; posteromedial to this crest, a second ridge extends posterolaterally. Together with the median pterygoid ridge, these features delimit a broad, gently concave palatal trough. The palatine contacts the vomer anteriorly, and has a relatively short contact with the maxilla laterally. It lacks the ventral, peg-like process present in *Plateosaurus* (Galton 1984). The palatines do not contact each other along the midline.

Pterygoid.—The pterygoid forms the posterior portion of the palate. It is a large, complex bone that, following Galton (1984), can be divided into a posterodorsally and laterally directed quadrate flange, a central region with the facet for the basipterygoid joint, a transverse process, and an anterodorsally extending palatal ramus. Posteriorly, the quadrate flange forms a deep vertical lamina of bone, which rises just lateral to the basipterygoid joint and is separated from the central region of the bone by a constriction. The basipterygoid joint is situated between the palatal and quadrate rami of the pterygoid; a dorsomedially facing facet on the pterygoid receives the distal end of the basipterygoid process of the basisphe-

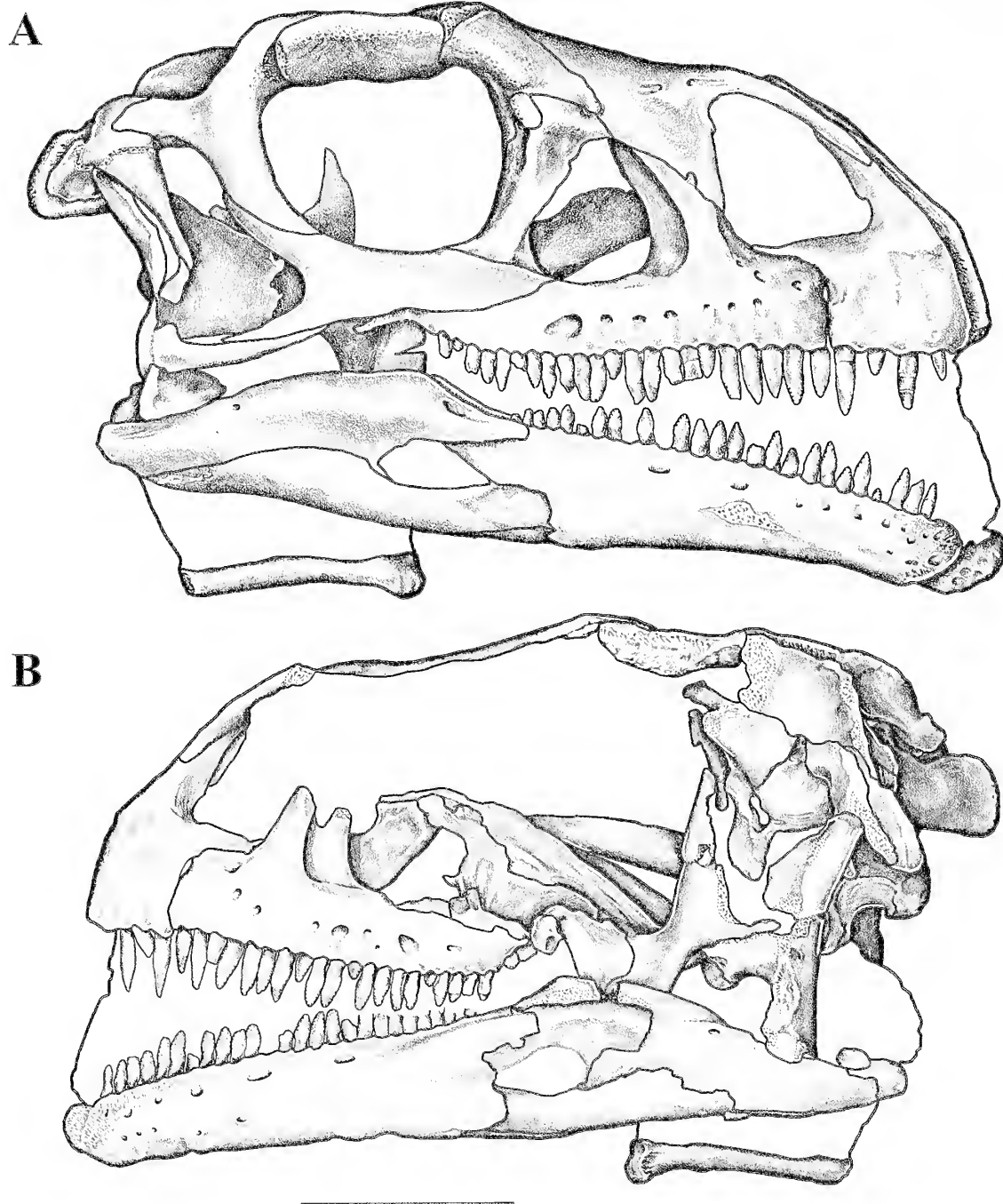
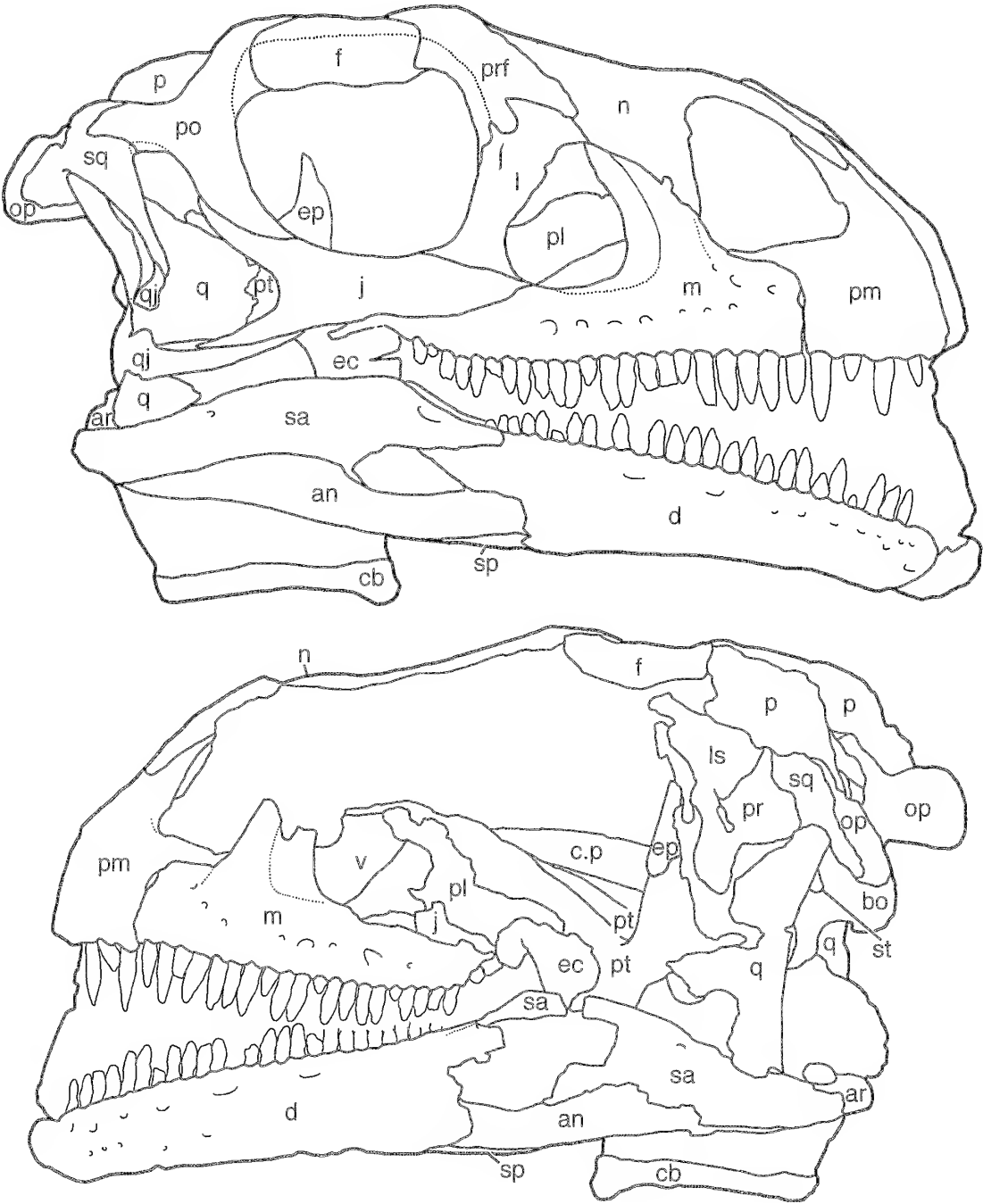


Fig. 5.—Skull of *Massospondylus carinatus* (BP/1/4934) in (A) right and (B) left lateral views with explanatory diagrams. Scale bar = 5 cm.



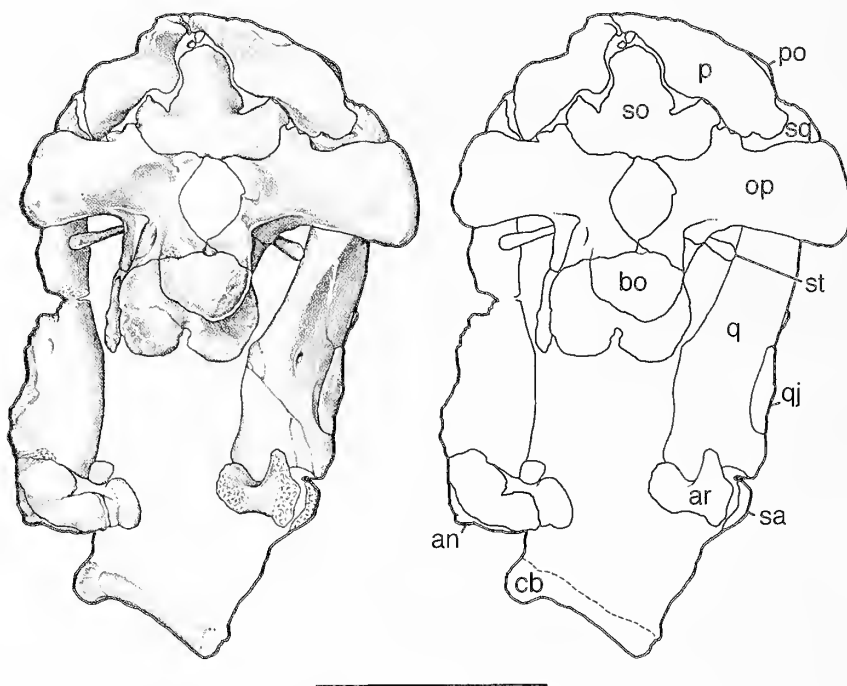


Fig. 6.—Skull of *Massospondylus carinatus* (BP/1/4934) in occipital view, with explanatory diagram. Scale bar = 5 cm.

noid. Unlike in *Plateosaurus*, there is no hook-like medial process of the pterygoid around the basiptyergoid process. The transverse process of the pterygoid overlaps the medial surface of the ectopterygoid. The palatal ramus of the pterygoid has a well-developed ventral plate, but tapers anteriorly to the level of the vomers and also forms a nearly vertical sheet of bone dorsomedially. The two palatal rami each form a distinct median crest and almost contact each other along the midline; anteriorly, they are wedged between the vomers. In BP/1/4779, the interpterygoid vacuity appears to be small, and the cultriform process of the parasphenoid is not fully exposed in ventral view.

Ectopterygoid.—The ectopterygoid has a slightly curved, rod-like lateral process with an anteroposteriorly broad end, which contacts the medial surface of the jugal. The expanded median portion of the ectopterygoid extends along the dorsal surface of the pterygoid to the transverse flange of the latter (which is partially exposed in lateral view on the left side of BP/1/4934), and meets the palatine dorsomedially.

Supraoccipital.—The supraoccipital makes up the dorsal margin of the foramen magnum and slopes anterodorsally, projecting slightly above the opening posteriorly. It contacts the occipital flanges of the parietals dorsally and laterally and the exoccipitals-opisthotics ventrolaterally. The supraoccipital is slightly wider transversely than tall dorsoventrally, being widest in its ventral portion, and

becomes narrower and more vertically oriented dorsally towards the skull roof. Dorsally, a median unossified gap (which was presumably filled by cartilage in life) is present between the posterolateral wings of the parietals and the dorsal apex of the supraoccipital. The supraoccipital bears a prominent median ridge for the attachment of the ligamentum nuchae. On either side, a lateral wing (which probably represents a fused epiotic) is separated from the main body of the supraoccipital by the posttemporal foramen for passage of V. capitis dorsalis on the suture between the supraoccipital and parietal. At the lateral end of this wing, there is an opening that is delimited by the parietal dorsally and the paroccipital process ventrally. We concur with Galton (1984) that this opening probably represents a much reduced posttemporal fenestra.

Orbitosphenoid.—The orbitosphenoid is documented by the well-preserved left element in BP/1/4934 and possibly by a displaced bone on the right side of the braincase in BP/1/4376. It contacts the laterosphenoid posteriorly. Two foramina are situated on the suture between the laterosphenoid and orbitosphenoid. The more anterior opening probably served for passage for N. oculomotorius (III), whereas the posterior one presumably represents the exit for N. trochlearis (IV).

Laterosphenoid.—The robust, anterolaterally projecting process of the laterosphenoid forms a transversely expanded dorsal condyle for contact with the frontal, parietal, and postorbital. A slender, anteromedially and dorsally directed process meets the frontal. The laterosphenoid broadly abuts the parietal dorsally. Posteroventrally, it contacts the anterior edge of the prootic and forms the anterodorsal margin of the trigeminal foramen. A depression on the ventrolateral aspect of the laterosphenoid probably received the dorsal end of the columella of the epipterygoid.

Prootic.—The prootic forms much of the lateral wall of the braincase, and broadly contacts the parietal dorsally. Its lateral surface is perforated by a large foramen for N. trigeminus (V), which is bounded posteriorly by a depression. A groove for ramus ophthalmicus of N. trigeminus (V_1) extends anterodorsally along the ventrolateral aspect of the laterosphenoid. Posteriorly, the prootic overlaps the

lateral aspect of the opisthotic at the base of the paroccipital process. Posterolaterally, behind the trigeminal foramen, the prootic bears a distinct, ventrally extending crista prootica.

Exoccipital-Opisthotic.—There is no clearly discernable suture between the exoccipital and opisthotic in the adult specimens, and they were presumably fused into a single element (otoccipital) as in most dinosaurs. In the juvenile specimen BP/1/4376, however, a suture between the two bones is still evident on the right side of the braincase. The exoccipital forms the lateral margin of the foramen magnum and the dorsolateral corner of the occipital condyle. It is perforated by a large posterior foramen and, anterior and slightly ventral to it, a smaller anterior opening, both of which served as passages for branches of N. hypoglossus (XII). Situated anteroventral to the hypoglossal foramina, the large metotic foramen presumably served for passage of N. glossopharyngealis, N. vagus, and N. accessorius (IX–XI) as well as V. jugularis interna. The paroccipital process is formed by the opisthotic, but the prootic contributes to the base of the process anteriorly. It projects posteriorly and ventrolaterally at an angle of about 45°, and its distal end is expanded dorsoventrally. The paroccipital process bears an anteroventral groove that houses the stapes.

Basioccipital.—The basioccipital forms the posterior portion of the floor of the braincase and narrowly separates the bases of the exoccipitals on the ventral margin of the foramen magnum. It contacts the exoccipitals dorsally and the parabasisphenoid ventrally and laterally. The basioccipital forms most of the occipital condyle, with the exoccipitals contributing only the dorsolateral corners of the condyle. The occipital condyle is deflected ventrally, and its articular surface is extended anteroventrally. It is separated from the remainder of the basioccipital by a distinct neck. The ventral margin of the condyle is in line with the long axis of the cultriform process (BP/1/4934). Below the occipital condyle, the basioccipital extends ventrally and forms the greater posterior portions of the stout and short basal tubera. In occipital view, the tubera are separated by a small but deep median recess and slightly diverge from each other ventrolaterally. The ventral ends of the tubera are distinctly rugose.

Basisphenoid-Parasphenoid.—As in most dinosaurs, the basisphenoid and parasphenoid are indistinguishably fused into a single element (parabasisphenoid), which forms the anterior portion of the floor of the braincase as well as the cultriform process, and contributes the small anterior portions of the basal tubera. The body of the compound bone bears an elliptical lateral depression; a small foramen at the anterior end of this depression represents the posterior opening of the canal for passage of A. carotis interna. The basipterygoid processes sharply

diverge from each other ventrolaterally, and are not connected by a deep transverse septum as in *Plateosaurus*. The distal ends of these processes are expanded for contact with the pterygoids. The long, transversely narrow cultriform process tapers anteriorly in lateral view.

Epipterygoid.—Both epipterygoids are preserved in BP/1/4934; the right element is complete except for its dorsal tip. The expanded ventral base of the epipterygoid broadly contacts the anterodorsal edge of the quadrate flange of the pterygoid. The lateral surface of the bone just above the sutural contact bears a series of fine vertical grooves. Dorsally, the epipterygoid narrows gradually into a rod-like columella, which is slightly recurved on the right element in BP/1/4934.

Stapes.—Both stapes are preserved in BP/1/4779 (Fig. 4) and in BP/1/4934 (Fig. 6). Based on the latter specimen, which retains the elements in situ, the stapes projected laterally and ventrally, as in *Plateosaurus* (Huene 1926). The stapedial shaft is slender and round in cross-section, slightly increasing in diameter towards its distal end. In BP/1/4779, the left stapes has been displaced from its original position, and its expanded proximal footplate is partially visible.

Scleral Ossicles.—The right orbit of BP/1/4376 contains a collapsed scleral ring composed of thin, plate-like ossicles, but little detail can be distinguished. Scattered scleral plates are also preserved in both orbits of BP/1/4779 and in the right orbit of BP/1/5241.

Mandible

This study confirms the statement by Gow et al. (1990) that the mandible of *Massospondylus* is not shorter than the skull, *contra* Crompton and Attridge (1986), who based their assessment on strongly dorsoventrally crushed specimens.

Dentary.—The dentary is the largest bone of the lower jaw. It is overlapped by the surangular posterodorsally, and overlaps the angular posteroventrally. The posterior end of the dentary is forked. The dentary forms the anterodorsal margin of the external mandibular fenestra. In the region of the symphysis, the lateral surface of the dentary bears numerous scattered neurovascular foramina. The splenial apparently covers much of the medial surface of the dentary. The first dentary tooth is set back from the anterior end of the bone by a distance equivalent to about one alveolar diameter, as in *Plateosaurus* and other basal sauropodomorph dinosaurs. A row of infralabial foramina (for passage of cutaneous branches of N. alveolaris inferior and associated vessels) extends parallel and just ventral to the alveolar margin of the dentary; the more posterior openings are slit-like and spaced further apart. A ridge extends obliquely anteroposteriorly

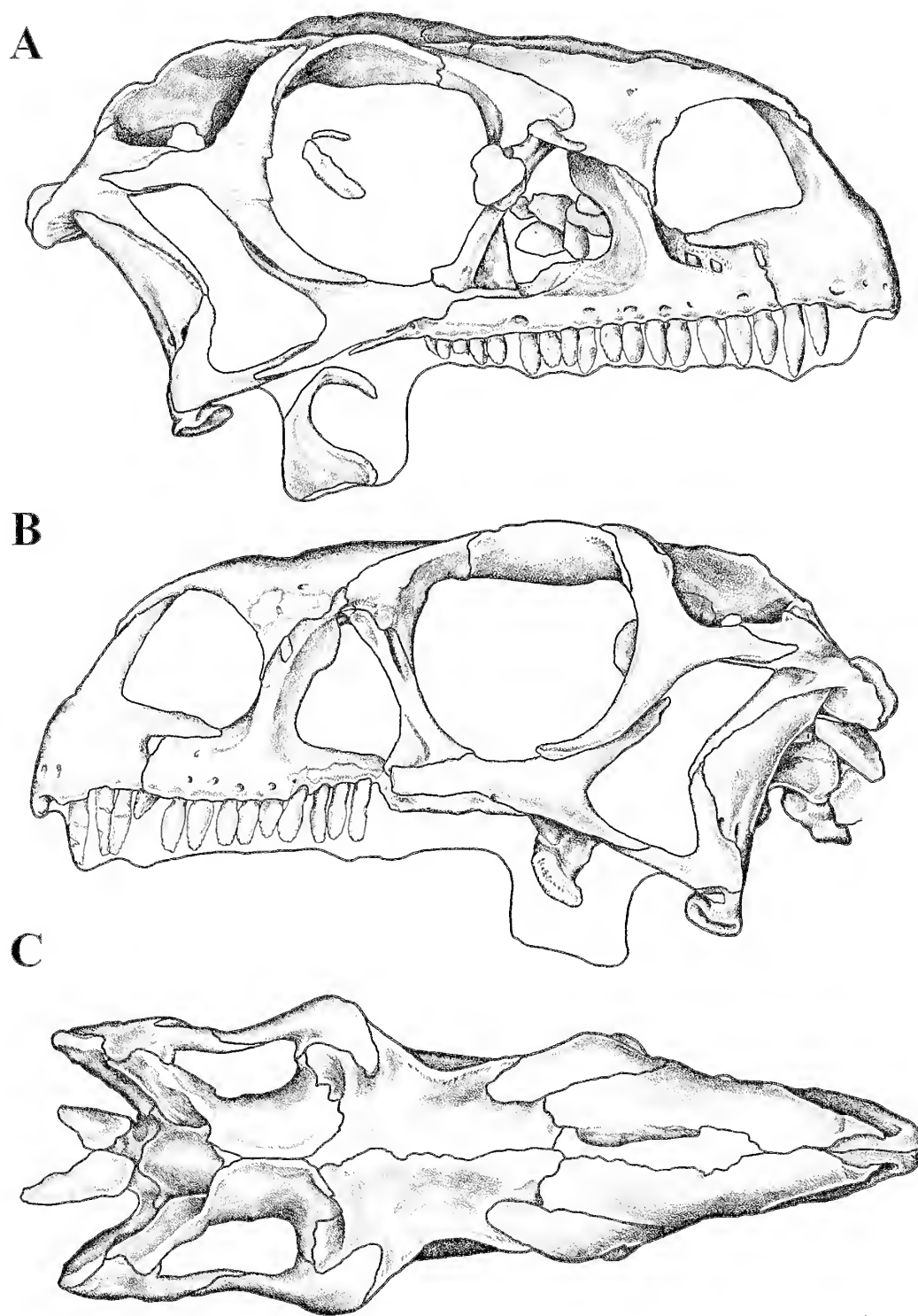
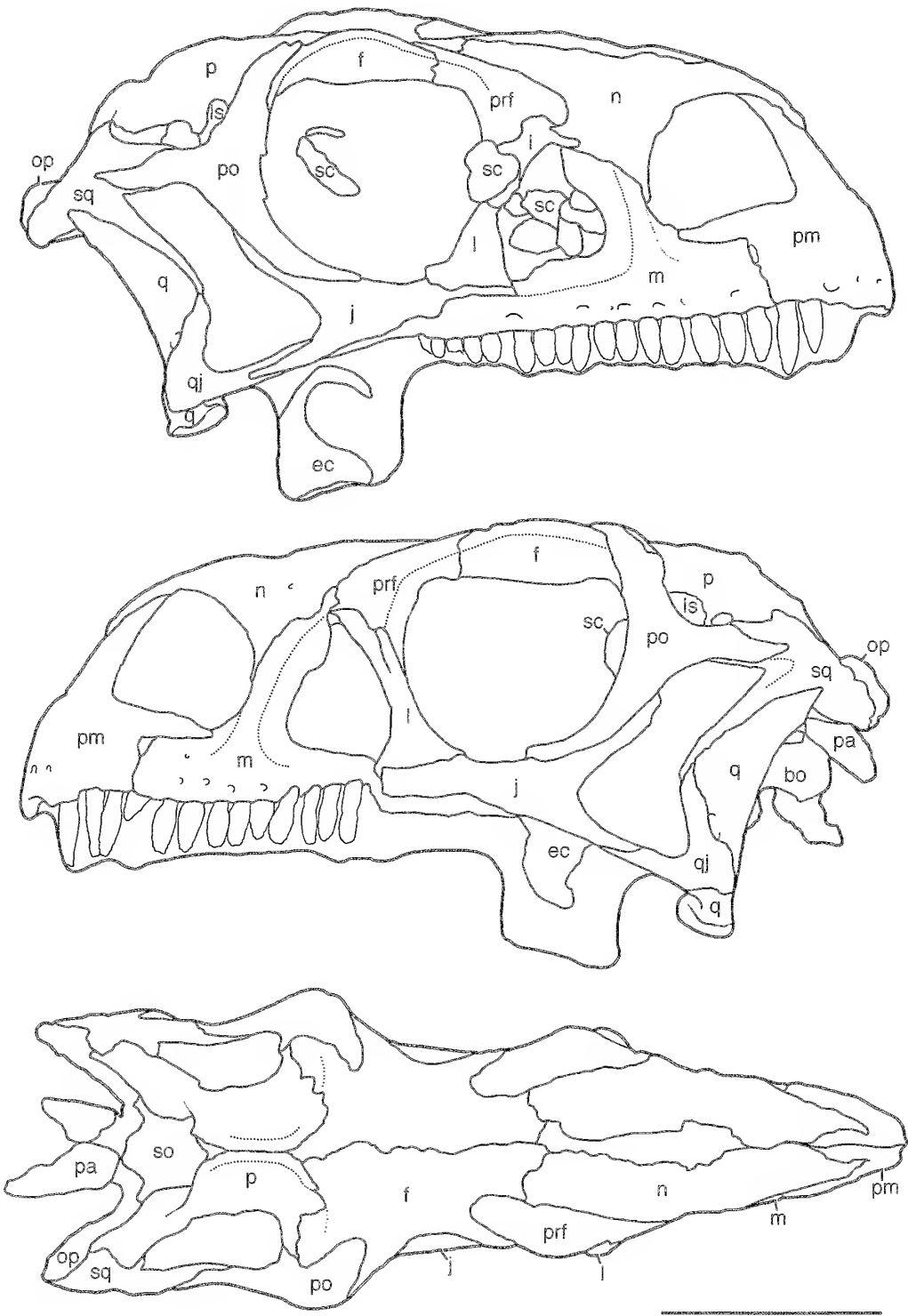


Fig. 7.—Skull (without mandible) of *Massospondylus carinatus* (BP/1/5241) in (A) right lateral, (B) left lateral, and (C) dorsal views, with explanatory diagrams. Scale bar = 5 cm.



below the posterior portion of the tooth row on the lateral surface of the dentary. It delimits a narrow, dorsolaterally inclined surface just lateral to the tooth row. The ventral margin of the dentary is gently concave in lateral view and forms a slight "chin" in the symphyseal region in BP/1/4376 and BP/1/4934. The rugose symphyseal facet of the dentary is nearly flat, and most of its perimeter is demarcated by sharp edges. There is no evidence for a beak covering the mandibular symphysis, as reconstructed by Crompton and Attridge (1986:fig. 17.6) in part based on the incorrect assumption of a disparity in length between the upper and lower jaws; furthermore, numerous scattered neurovascular foramina on the symphyseal portion of the dentary are also found in many archosaurian reptiles that lack a rhamphotheca.

Coronoid.—The slender coronoid bone is clearly visible only in BP/1/4376. It extends posteromedially to overlap the medial aspect of the anterodorsal portion of the surangular.

Surangular.—The large surangular forms the posterodorsal portion of the mandibular ramus. The dorsal margin of the jaw rises anteriorly from the jaw joint up to a low peak (coronoid eminence) and then descends again to the level of the alveolar margin of the dentary. It is medially thickened. The surangular also forms most of the dorsal margin of the external mandibular fenestra. It overlaps the dentary anteriorly and the articular posteriorly. A large anterior surangular foramen, which probably transmitted cutaneous branches of N. alveolaris inferior (Oelrich 1956), is situated ventral or slight anterior to the coronoid eminence. Just behind the foramen on the dorsolateral surface of the surangular, a pronounced longitudinal ridge probably marks the insertion for part of M. adductor mandibulae externus and possibly M. pseudotemporalis (Galton 1985). A small posterior surangular foramen is situated at the posterior end of this ridge. The suture between the surangular and angular extends in a shallow depression along the posterolateral aspect of the mandibular ramus in BP/1/4934. Medially, the surangular forms the lateral wall of the adductor fossa.

Angular.—The angular is relatively narrow and short. It forms the ventral margin of the external mandibular fenestra. Anteriorly, the angular is overlapped by the dentary, and it overlaps the surangular posteriorly. It contacts the prearticular medially. The ventral edge of the angular is rounded.

Prearticular.—The long, thin prearticular forms the ventral margin of the adductor fossa, and becomes expanded toward its anterior end. Its posterior contact with the articular cannot be identified on the available specimens.

Articular.—The articular projects medially from the medial surface of the mandibular ramus. Posteriorly, it

forms a long, slender retroarticular process (which is completely preserved only on the left mandibular ramus of BP/1/4934). Anterolaterally, a thin sheet of the surangular overlaps the retroarticular process and, medially, the process is partially covered by the prearticular. The articular bears the mandibular facet for the jaw joint, which is situated below the level of the alveolar margin of the dentary in lateral view.

Splénial.—The splénial probably covered much of the lingual surface of the dentary. Posteriorly, it is overlapped by the coronoid dorsally and the prearticular ventrally. Unfortunately, the anterior portion of the splénial is not well preserved in any of the available specimens.

Hyoid

An elongate, gently curved, and rod-like bone is preserved ventral to the posterior portion of the right mandibular ramus in BP/1/4934 and both rami in BP/1/4376. It presumably represents ceratobranchial 1 (cornu branchiale I). The anterior and posterior ends of this element are expanded and blunt.

Dentition

The marginal dentition of *Massospondylus* is moderately heterodont. The teeth have thecodont implantation. The dentary tooth rows are situated lingual to the premaxillary and maxillary tooth rows. Posteriorly, the maxillary tooth row extends well beyond the dentary tooth row in BP/1/4934. There is no evidence of tooth-to-tooth wear. As in other basal sauropodomorphs (e.g., *Plateosaurus*; Galton 1984, 1985), the individual tooth crowns are labiolingually compressed, taller than wide mesiodistally, not recurved, and more or less symmetrical in labial view (Fig. 8). On well-preserved tooth crowns, a faint median ridge extends vertically along the vertically gently convex labial surface of the crown, terminating in an apical denticle. Each tooth is slightly constricted between the root and crown. The mesial and distal carinae are coarsely serrated with denticles that project apically at an angle of about 45° relative to the carina, much as in other basal sauropodomorph dinosaurs. The denticles are restricted to the apical portion of the tooth crown. There are up to 11 denticles per crown in the adult specimens and up to 13 in the juvenile specimen BP/1/4376. On some teeth, the denticles along the distal carina extend further toward the root than do those along the mesial carina, but this condition could not be checked on many teeth.

There are four premaxillary teeth, of which the fourth typically has the tallest crown. They are the tallest teeth in the upper jaw; the disparity in size between the premaxillary and maxillary teeth is particularly evident in BP/1/4376. The premaxillary teeth also differ from the maxillary ones in being slightly further separated from

each other so that there is less overlap between adjacent tooth crowns and both carinae of each crown are visible in labial view. They are set slightly obliquely in the premaxilla so that their mesial carinae face more lingually and their distal carinae more labially. (This condition is also present on at least some of the maxillary teeth.) This arrangement makes the premaxillary teeth appear more slender and conical in labial view.

There are 14 teeth plus at least one additional alveolus in the right maxilla of BP/1/4376, 17 teeth or alveoli in the right maxilla of BP/1/5241, and 22 teeth in either maxilla of BP/1/4934. The maxillary tooth crowns decrease in height towards the posterior end of the tooth row.

BP/1/4934 has 26 teeth or alveoli in each dentary. The dentary teeth are similar in shape to but less tall than those of the maxilla; their crowns slightly decrease in height posteriorly.

Gow et al. (1990) commented on aspects of tooth replacement in the skulls of *Massospondylus* described here, obviating the need for further discussion.

DISCUSSION

Although the interrelationships of basal sauropodomorph dinosaurs have long been the subject of discussion in the literature (Huene 1932; Galton 1990; Sereno 1999; Benton et al. 2000), Yates (2003B) and Yates and Kitching (2003) were the first to publish comprehensive phylogenetic analyses of these taxa. Yates (2003B) argued that the basal sauropodomorph dinosaurs traditionally grouped together as Prosauropoda actually form a paraphyletic array of successive sister-taxa to Sauropoda. He showed that constraining the parsimony analysis to retain Prosauropoda (including *Saturnalia*; Langer et al. 1999) resulted in trees 24 steps longer than the most parsimonious trees with a length of 309 steps. Sereno (1999) had argued in support of the monophyly of Prosauropoda. Yates's reanalysis of Sereno's character-taxon matrix, however, demonstrated that only 3 out of 19 characters would unambiguously support prosauropod monophyly, and Yates raised additional issues related to the exclusion of a number of sauropodomorph taxa from that dataset. Later, Yates and Kitching (2003) restricted Prosauropoda to *Riojasaurus* (*Plateosaurus* (*Coloradisaurus* (*Massospondylus* + *Lufengosaurus*))), excluding *Saturnalia*, *Thecodontosaurus*, and *Efraasia* from that grouping, and reinterpreted *Anchisaurus* as the most basal member of Sauropoda.

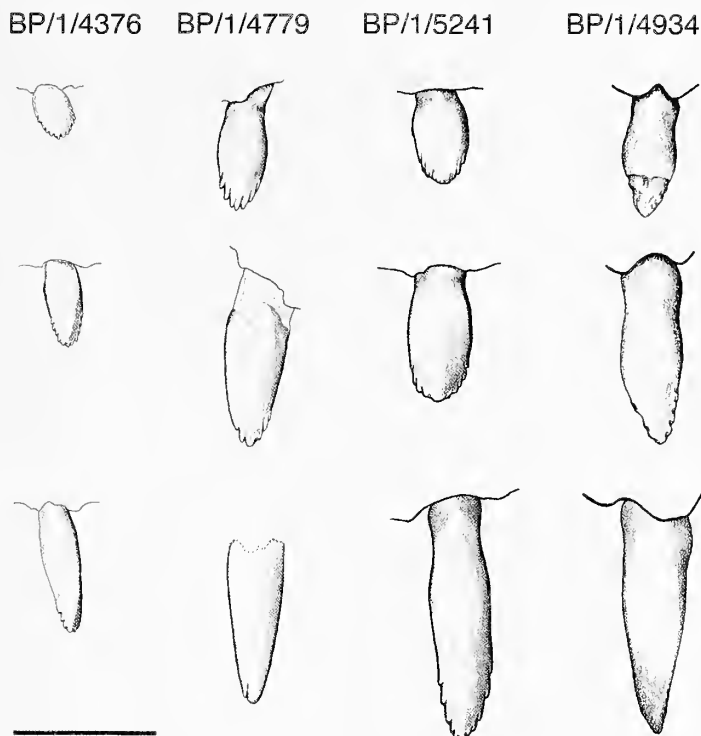


Fig. 8.—Camera-lucida drawings of the crowns of selected teeth in labial view from the skulls of *Massospondylus carinatus* described in this study. **Top row:** posterior maxillary teeth. **Center row:** anterior maxillary teeth (at the level of the dorsal process of the maxilla). **Bottom row:** premaxillary teeth. Scale bar = 1 cm. **BP/1/4376:** Maxillary teeth 11 and 5 and premaxillary tooth 3 (all from right side); **BP/1/4779:** Maxillary teeth 10 and 7 and premaxillary tooth 2 (all from right side); **BP/1/4934:** Maxillary teeth 17 (from left side) and 4 (from right side) and premaxillary tooth 4 (from left side); **BP/1/5241:** Maxillary teeth 13 and 6 and premaxillary tooth 4 (all from right side).

The most parsimonious trees recovered by Yates (2003B) grouped *Massospondylus* with either *Lufengosaurus* or *Yunnanosaurus* from the Lower Jurassic Lower Lufeng Formation of Yunnan, China. More recently, Yates and Kitching (2003) considered *Massospondylus* the sister-taxon of *Lufengosaurus* and placed *Coloradisaurus*, from the Upper Triassic Los Colorados Formation of Argentina (originally described under the preoccupied generic nomen *Coloradia*; Bonaparte 1978), as the sister-taxon to the clade *Massospondylus* + *Lufengosaurus*. They united these three taxa in a grouping Massospondylidae. Unfortunately, the structure of the skull in *Lufengosaurus* is still poorly documented (Young 1941), preventing more detailed comparison with *Massospondylus*. Two character-states for *Massospondylus* in the online appendix for Yates and Kitching (2003) must be revised based on the present study. The state for character 19 (pointed posterolateral process of nasal overlapping lacrimal) is 0 rather than 1; although the nasal overlaps the lacrimal posterolaterally it does not form a distinct posterolateral

process as in *Plateosaurus*. Character 24 (jugal contribution to margin of antorbital fenestra) appears to be polymorphic in *Massospondylus*. Furthermore, the missing states for characters 37 through 40 for *Massospondylus* in the online appendix for Yates and Kitching (2003) can now be determined: The quadrate foramen is deeply incised into the quadrate (37.0), the proportion of the length of the quadrate to the length of the base of the pterygoid flange is less than 70 percent (38.1), the jugal process of the ectopterygoid is gently curved (39.0), and there is no pneumatic fossa on the ventral surface of the ectopterygoid (40.0). Finally, the state for character 61 (length of retroarticular process relative to depth of mandibular ramus below glenoid) is 1 rather than 0, and that for character 63 (orientation of dentary tooth crowns) is 0 rather than 1. Introducing these changes in the character-taxon matrix and reanalyzing the modified matrix using the parsimony option in PAUP 4.0b10 (Swofford 1998) did not affect the tree topology recovered by Yates and Kitching (2003).

With the exception of *Plateosaurus* (Huene 1926; Galton 1984, 1985; Yates 2003A), the cranial structure of most basal sauropodomorph dinosaurs remains poorly known or documented. Only limited information has been published so far for *Anchisaurus* (Galton 1976), *Coloradisaurus* (Bonaparte 1978), *Efraasia* (Galton and Bakker 1985; Yates 2003A), *Lufengosaurus* (Young 1941), *Mussaurus* (Bonaparte and Vince 1979), *Riojasaurus* (Bonaparte and Pumares 1995), and *Thecodontosaurus* (Benton et al. 2000; Yates 2003B). This dearth of comparative data makes it difficult to identify autapomorphic cranial features for *Massospondylus*. One feature cited by Sereno (1999) is the proportionately greater width of the skull compared to that in other basal sauropodomorph taxa such as *Plateosaurus*. The greatest transverse width of the skull of *Massospondylus* exceeds its dorsoventral height by at least 10 percent. *Massospondylus* further differs from *Plateosaurus* and at least some other basal sauropodomorph taxa in the proportionately large size of the orbit and shorter antorbital region of the skull even in adult specimens (Gow et al. 1990). Galton (1990:339) cited the "centrally situated and almost vertical" dorsal process of the maxilla as a derived feature of Massospondylidae, which only comprised *Massospondylus* in his usage. Although the dorsal process is not centrally situated at least in the specimens of *Massospondylus* described here, it is tall and nearly vertical. The maxilla of *Mussaurus* from the Upper Triassic (Norian) El Tranquilo Formation of Santa Cruz, Argentina, also has a tall, nearly vertical dorsal process and an anteroposteriorly narrow medial sheet (Bonaparte and Vince 1979). The anteroposteriorly narrow medial sheet of the maxilla in *Massospondylus* is similar to that in more basal sauropodomorph taxa such as *Efraasia* (Yates 2003A) from the Upper Triassic (Norian) Löwenstein Formation of southern Germany and

Thecodontosaurus (Yates 2003B) from the Upper Triassic (?Norian) of southwest England but differs from the anteroposteriorly broad medial sheet in *Plateosaurus*. The prefrontal has a long posterior process along the dorsal margin of the orbit, similar to the condition in *Lufengosaurus* (Young 1941) and in *Plateosaurus*. The lacrimal of *Massospondylus* resembles that of *Plateosaurus* in the development of a lateral sheet overhanging the posterodorsal corner of the antorbital fenestra. The dorsolateral aspect of the lacrimal in *Massospondylus* bears a distinct ridge, which is continuous with a knob on the lateral surface of the prefrontal. Barrett (pers. comm. 2004) observed similar features in *Lufengosaurus*, but they are not evident in Young's (1941) account.

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ERRATUM

Wible, John R., and Timothy J. Gaudin. On the cranial osteology of the yellow armadillo *Euphractus sexcinctus* (Dasypodidae, Xenarthra, Placentalia). *Annals of Carnegie Museum*, 73(3):117–196.

In the original published title, the species name of the yellow armadillo was incorrectly spelled *E. sexcintus*. For the purposes of citation, the above title with the corrected spelling, *E. sexcinctus*, should be used.

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